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P. E. CRAY

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BY

PETER EDGAR CRAY

Bath Academy of Art, Corsham

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SYNOPSIS

The present work incorporates a revision of part of the mammalian fauna of the Headon Beds (Upper Eocene) of Hampshire and the Isle of Wight.

Stratigraphical and historical aspects of the main mammal-yielding horizons in the Headon Beds are presented, together with provisional lists of the complete mammalian fauna.

Marsupialia, Insectivora, Primates, Creodonta and Carnivora are considered in the systematic descriptions. Fourteen species of mammals are described, of which four are new. Two new insectivore genera, *Scraeva* and *Arvaldus* are referred to the Nyctitheriidae. *Arvaldus* is known from a single species, *A. stintoni;* two species of *Scraeva* are recognised, *S. hatherwoodensis* and *S. woodi*. A partial upper dentition has been referred to the pantolestid insectivore *Opsiclaenodon major*, previously known only from the lower dentition. Well preserved material of a new species of *Dyspterna*, *D. hopwoodi*, supports reference of the genus, formerly almost a *nomen dubium*, to the Pantolestidae, and confirms the close relationship of *Dyspterna* and *Opsiclaenodon*. *Heterohyus* sp., *Adapis parisiensis* and *Pseudoloris parvulus* all constitute new records from the Headon Beds.

The evidence from those mammals given detailed study, indicates that at present the Upper Headon Beds are best grouped provisionally with the Lower Headon Beds in the Upper Eocene (Lower Ludian). The Eocene/Oligocene boundary should be sited at some position above the Upper Headon Beds.

I. INTRODUCTION AND ACKNOWLEDGEMENTS

The first mammals recorded from the Headon Beds were listed by Wood (1844); these specimens, listed again by Charlesworth (1845), came from the Lower Headon Beds of Hordle Cliff. In a further paper, Wood (1846–47) listed and excellently illustrated this and further material from Hordle Cliff. The first record of mammals from the Upper Headon Beds of Headon Hill was in a stratigraphical account by Prestwich (1846). The earliest detailed description of mammals from the Headon Beds was by Owen (1848).

In a preliminary paper in 1848, Barbara, Marchioness of Hastings recorded mammals from Hordle Cliff. She published, in 1852 and 1853, the results of six years' collecting from this section. In addition to mammals, the Marchioness recorded fish, reptile and bird material, together with valuable information about occurrence and preservation. Also in 1852, Wright recorded an isolated mandible from the Lower Headon Beds of Headon Hill; this was described by Owen (1857a). Some of the Marchioness of Hastings' specimens were described by Owen (1857b) and Davies (1884).

The only detailed systematic work was by Lydekker in his 'Catalogue of the Fossil Mammalia in the British Museum', published in five parts between 1885–87. The Headon Beds material was incompletely and sometimes inaccurately listed, but Lydekker made a valuable contribution, consolidating Owen's work and describing more of the Marchioness of Hastings' collection. Some of Lydekker's results were published as a few short papers (1884, 1885b, 1885d).

Stehlin's monograph 'Die Säugetiere des schweizerischen Eocaens' (1903–16) contained critical discussions of some of the Headon Beds material. In a faunal paper, Stehlin (1910) listed sixteen species from Hordle Cliff. Depéret (1917), in a revision of the mammalian fauna of Euzet-les-Bains, listed four species from Headon Hill and sixteen from Hordle Cliff. Contributions on aspects of the fauna were made by Cooper (1910, 1925, 1926, 1928). The most recent work, on isolated genera, has been by Butler (1946), Simons (1961) and Franzen (1968).

The present work comprises a revision of part of the mammalian fauna of the Headon Beds. In the faunal lists, identification of Rodentia, Perissodactyla and Artiodactyla is tentative; these elements of the Headon fauna have not yet been studied in detail.

Throughout the systematics, the age of the Headon Beds is considered provisionally as Upper Eocene (Lower Ludian). This problem is discussed later in the light of the evidence afforded by study of the mammals.

Traditional stratigraphical nomenclature has been retained for the subdivision of the succession; as the purpose of the present work is primarily palaeontological, no attempt has been made to bring this nomenclature into concordance with modern international stratigraphical practice.

The registration numbers of museum specimens are prefixed as follows:

B.M.	British Museum (Natural History)
S.M.	Sedgwick Museum, Cambridge
G.S.M.	Geological Survey Museum

D.M.S.W.	D.M.S. Watson collection; now in University Museum of Zoology, Cambridge

In addition, some specimens are from the private collection of Mr F. C. Stinton; these are prefixed F.C.S. Where differentiation of several specimens grouped under a single museum registration number has been necessary, numbers in parentheses have been added after the museum registration number.

In the tables of measurements, all dimensions are in millimetres. Antero-posterior length (a-p) and transverse width (trs) are maximum values. Measurements in parentheses represent approximations, based on damaged teeth or taken from roots.

I am very grateful to Dr R. J. G. Savage, not only for supervision of the initial research, but also for his continued encouragement, advice and stimulating discussion since that time. I also wish to thank him for so readily making available his personal library and for critically reading the draft manuscript. I am indebted also to Dr D. E. Russell for much encouragement and advice, for his generosity in permitting examination of type specimens and manuscript from unpublished work and for critically reading the draft manuscript.

My thanks are due to the following for facilities to study collections or for the loan of specimens: Dr A. J. Sutcliffe and Dr R. Hamilton of the British Museum (Natural History); Dr C. L. Forbes and Dr R. B. Rickards and their predecessor Mr A. G. Brighton of the Sedgwick Museum, Cambridge; Professor J.-P. Lehman of the Muséum National d'Histoire Naturelle, Paris; Mr J. M. Edmonds of the University Museum, Oxford, and the late Mr A. T. Grapes of the Museum of Isle of Wight Geology, Sandown, Isle of Wight. Thanks are due also to Mr F. C. Stinton for the loan of specimens from his private collection.

I am indebted also to Dr J. W. Murray for helpful discussion of certain aspects of the stratigraphy; to Dr J. M. Pallot for the processing and identification of pollen samples and to Dr N. Edwards for much helpful discussion and for the use of information from unpublished manuscript.

My thanks are due also to Mr J. Martin for the drawing of figs 9, 10 and 12, and to Mr R. J. Godwin for the photography.

The initial research, of which this paper forms part, was carried out during the tenure of a studentship from the (then) Department of Scientific and Industrial Research. This grant and the facilities offered by the late Professor W. F. Whittard in the Geology Department of the University of Bristol are gratefully acknowledged.

II. FOSSIL HORIZONS AND FAUNAL LISTS

(a) Introduction

A general account of the geological structure and Tertiary stratigraphy of the Hampshire Basin can be found in Chatwin (1960). A brief summary of the stratigraphical subdivisions and geographical distribution of the Headon Beds is given by

Curry (1958a). Useful introductory summaries of the stratigraphy of classic Tertiary coastal sections in the area are presented by Curry (1958b and 1958c).

Mammalian material has been obtained from the brackish and freshwater Lower and Upper Headon Beds at two main localities (Fig. 1): on the mainland at Hordle Cliff (Lower Headon Beds) and on the Isle of Wight at Headon Hill (Lower and Upper Headon Beds).

The only record of a fossil mammal from the predominantly marine and estuarine Middle Headon Beds is ?*Zygorhiza juddi* (Seeley), a cetacean (Kellogg, 1936 : 176). The specimen, a caudal vertebra, was obtained from the purely marine basal Brockenhurst Bed, at Royden near Brockenhurst (Judd, 1881).

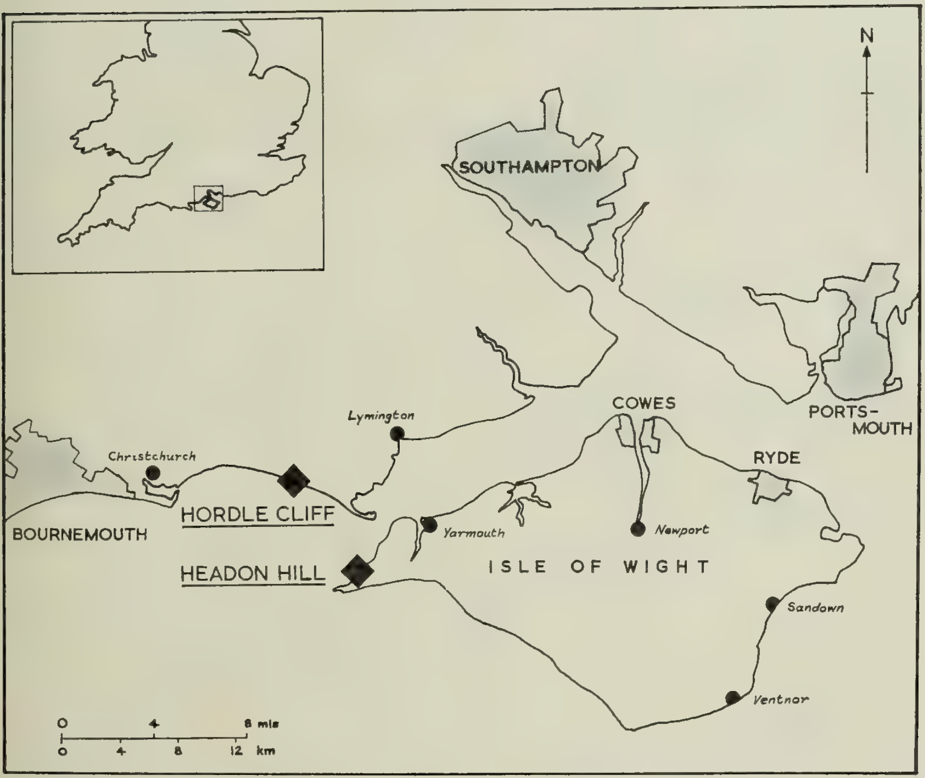
N
SOUTHAMPTON
Lymington
COWES
PORTS-MOUTH
RYDE
Christchurch
HORDLE CLIFF
BOURNEMOUTH
Yarmouth
Newport
HEADON HILL
ISLE OF WIGHT
Sandown
Ventnor
0 4 8 mls
0 4 8 12 km

FIG. 1. Map showing the two main mammal-yielding localities of Hordle Cliff and Headon Hill.

(b) Horizons at Hordle Cliff, Hampshire

(i) Introduction

In Christchurch Bay, continuous cliffs from Mudeford eastwards to Milford-on-Sea expose excellent sections of the Barton and Lower Headon Beds, with representatives of the Bracklesham and Middle Headon Beds. The succession dips gently eastwards. The cliffs, capped by Pleistocene Plateau Gravel, range in height from 10–30 m, and are interrupted in places by small ravines or 'bunnies' as they are known locally.

The Headon Beds outcrop at Hordle Cliff (= Hordwell Cliff, the old spelling, still used occasionally) from east of Barton-on-Sea (just west of Beckton Bunny) to Milford-on-Sea (figs 2–4). In some early accounts, the section from Beckton Bunny to Long Mead End was known as Beacon Cliff, and 'Hordle Cliff' was restricted to the section from Long Mead End to Milford-on-Sea. However, for many years, all the section containing the outcrop of the Headon Beds (including Beacon Cliff) has been described as Hordle Cliff; this latter established usage is followed here.

The lowest part of the Headon Beds, the Mammal Bed, occurs beneath the Plateau Gravel west of Beckton Bunny, running obliquely down the cliffs as a vertical scar-like face, to reach sea level just east of Long Mead End. The Crocodile Bed forms a similar, higher scar. The highest beds, the *Limnaea* Marl and associated beds, outcrop as a lens below the Plateau Gravel, just east of Hordle House. At Paddy's Gap, the Milford Marine Bed represents the basal Middle Headon Beds. Over most

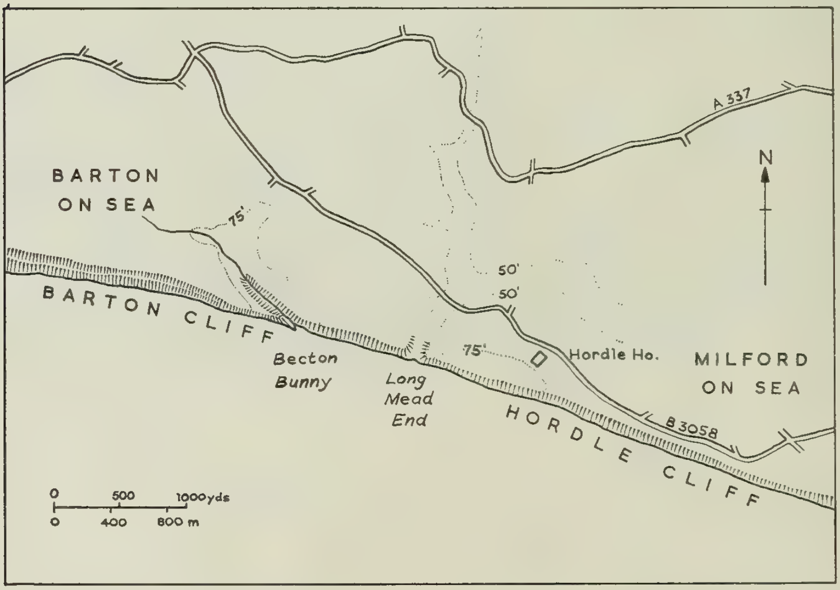

FIG. 2. Locality map of Hordle Cliff, Hampshire.

of the section, there is usually a veneer of talus and at several localities, notably at Long Mead End, there is extensive slipping; thus individual beds can be traced laterally only with difficulty.

The bulk of the museum material was obtained from the Lower Headon Beds of this area, mainly in the middle of the 19th century. The first recorded specimens, apparently derived from the Crocodile Bed, were listed by Searles Wood in 1844. The most significant contributions were made by Barbara, Marchioness of Hastings who described in 1852 and 1853 the results of six years' collecting from these beds. She made extensive collections of vertebrate remains from two main horizons, the Mammal Bed and the Crocodile Bed. Unfortunately, her material was not accurately labelled and the specimens, purchased by the British Museum (N.H.) in 1855, usually only bear the information 'Upper Eocene, Hordwell', or are listed in Lydekker's Catalogue as 'from the Headon Beds of Hordwell'. However, from the Marchioness's accounts (1848; 1852; 1853), it appears that the major mammal-yielding horizons were highly fossiliferous pockets within the Crocodile Bed. Regardless of the name given to it by later collectors, the Mammal Bed seems to have been much less important quantitively.

Many museum specimens still bear adhering matrix; this is very variable, comprising white and grey sands both coarse and fine, fine greenish-blue sandy clays, sometimes shelly, and coarse brown clayey sands. It is probable that most of the specimens with adhering greenish-blue sandy clay were obtained from the Mammal Bed, but the other lithologies are much less diagnostic. Also, matrix is no longer preserved on a considerable number of specimens. Consequently, material from these two main horizons cannot be reliably distinguished and is here considered collectively.

The Marchioness of Hastings also listed (1852; 1853) several apparently minor mammal-yielding horizons. Material from these levels was referred to only as 'bones and teeth of mammals' and 'rodent jaws'. None of the Marchioness's collection indicates derivation from any of these horizons, and the specimens, if still preserved, are presumably incorporated in the Mammal/Crocodile Bed sample. These well-defined horizons are listed below for completeness.

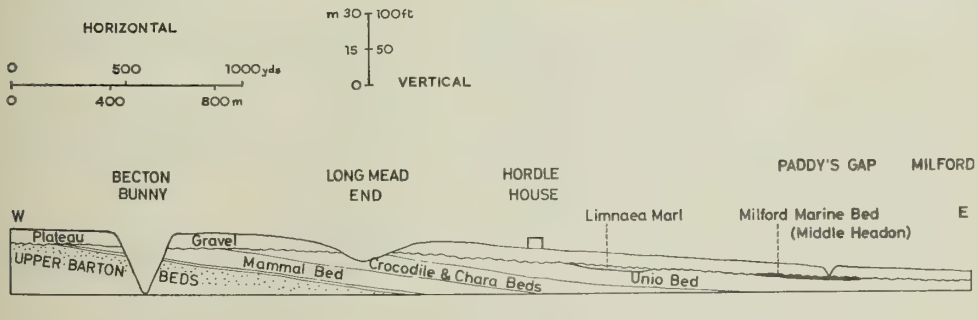

FIG. 3. Cliff section of the Lower Headon Beds at Hordle Cliff, Hampshire. Based on Curry, 1958b, fig. 1.

Little mammalian material has been found for many years from Hordle Cliff; one specimen, a mandible, was found in 1926. All these sites were examined during 1961–62, but little material was found.

All mammal-bearing horizons from the Lower Headon Beds of Hordle Cliff are listed below, together with the mammalian material derived from them. Relevant parts of the Marchioness of Hastings' descriptions are given; these quotations are taken mainly from the Marchioness's earlier detailed account (1852) in French, and not from her later, slightly modified English transcript (1853) of this paper.

(ii) Lower Headon Beds

Rodent Bed

Stratigraphy

At Hordle Cliff, a thin layer of dark clayey sand occurs almost at the top of the Lower Headon Beds, resting on a comminuted shell bed, the latter usually being known as a *Limnaea* Marl. The clayey sand is overlain by about 1 m of marl—the highest horizon referred to the Lower Headon Beds—which is stained and altered by the overlying Plateau Gravel. This *Limnaea* Marl and the overlying beds are of restricted lateral extent and outcrop immediately beneath the subhorizontal capping of Plateau Gravel just east of Hordle House, continuing eastwards for some 275 metres. Further westwards, these beds, if originally present, have been removed by erosion, although eastwards they wedge out, since at Paddy's Gap, basal Middle Headon sands rest directly on the Lower Headon *Unio* Beds.

These beds—the uppermost marl, the thin dark clayey sand and the underlying *Limnaea* Marl—were first described by the Marchioness of Hastings. Referring to her bed 1 (1852 : 194), she stated, 'La partie supérieure et principale de cet lit est entièrement dépourvue de fossiles; mais à environ un demi-mille de l'endroit où ces couches surgissent, une petite bande d'argile d'une couleur foncée, d'environ 4 pouces, se montre à la base du lit; . . .' The Marchioness listed extensive vertebrate remains, including rodent material, from this bed: '. . .; cette bande contient beaucoup de débris, mais généralement très comprimés et très fragiles. On y trouve de petites mâchoires de rongeurs, des portions de carapace et de plastron d'*Emys*, des dents et parfois beaucoup de fragments d'os de Crocodile, des vertèbres de serpents, et rarement des dents et des os de *Mammifères*.' The exact position of this small band of dark coloured clayey sand was left in no doubt by the Marchioness by her reference to the underlying *Limnaea* Marl.

Tawney & Keeping, in their detailed stratigraphical account of Hordle Cliff (1883 : 567), gave a similar description of the beds but listed only 'serpents' vertebrae' from the *Limnaea* Marl. The Marchioness's extensive list of vertebrate material from the dark clayey sand was omitted.

However, information given by Gardner, Keeping & Monckton (1888 : 596) is largely in agreement with the observations of the Marchioness; these authors recorded '. . . serpents' vertebrae, rodents' teeth, etc.' from the dark clayey sand.

The term 'Rodent Bed' was first used by Reid, (*in* Reid & Groves, 1921). This account, as Curry has observed (1958a : 69), was very confused, but Chandler who worked with Reid stated (1925 : 4) that the term was applied by him to the *Limnaea* Marl. Chandler, three years earlier (1922 : 224), recorded a section just to the east of Hordle House, in which she listed the '*Limnaea* Marl or Rodent Bed'; no vertebrate remains were noted by her from this horizon. Immediately above the *Limnaea* Marl she recorded 'a dark streak 2 in., with teeth, bones.' This latter account by Chandler was thus essentially the same as the original description by the Marchioness of Hastings. Recently, Curry (1958a and 1958b) adhered to the terminology of Reid and Chandler, referring to the *Limnaea* Marl as the 'Rodent Bed'.

Recently obtained specimens, part of an unreturned Sedgwick Museum loan, are labelled, 'Rodent Bed, Hordle Cliff, Hampshire'. This material may have been derived from the *Limnaea* Marl (Rodent Bed, *sensu stricto*) by Reid in the early years of the present century. Part of this material belonged to C. F. Cooper and may have been collected by him between the years 1910–30. However, the Marchioness's original description and some later accounts point to a possible derivation, at some time, from the overlying dark clayey sand; recent fieldwork has tended to confirm this latter view. Owing to the uncertainty of the precise horizon from which the

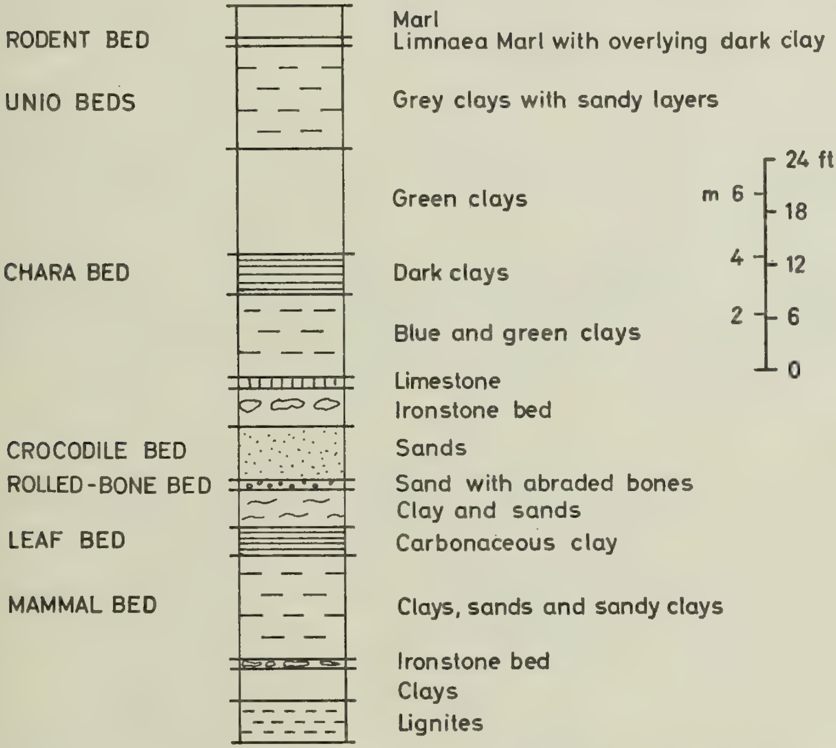
RODENT BED
UNIO BEDS
CHARA BED
CROCODILE BED
ROLLED-BONE BED
LEAF BED
MAMMAL BED
Marl
Limnaea Marl with overlying dark clay
Grey clays with sandy layers
Green clays
Dark clays
Blue and green clays
Limestone
Ironstone bed
Sands
Sand with abraded bones
Clay and sands
Carbonaceous clay
Clays, sands and sandy clays
Ironstone bed
Clays
Lignites
m 6
4
2
24 ft
18
12
6
0

FIG. 4. Generalised succession of the Lower Headon Beds at Hordle Cliff, Hampshire. Modified from Gardner, Keeping & Monckton, 1888, fig. 4.

material was obtained, the term 'Rodent Bed' (*sensu lato*) is applied collectively here to the *Limnaea* Marl and the overlying thin dark clayey sand.

Mammalian fauna

Almost all the mammals collected from the Rodent Bed found their way to Cambridge. In 1932, C. F. Cooper, then Superintendent of the University Museum of Zoology, arranged for the material to be borrowed by M. A. C. Hinton who intended to describe them, presumably in one of his publications on rodents. Following Hinton's death in 1961, Dr R. J. G. Savage, his scientific executor, found the specimens but none of Hinton's relevant notes or manuscript. This material comprised several boxes of small isolated teeth, some of which were roughly sorted, and a few other boxes filled with unsorted bone fragments and teeth of small mammals, reptiles and fish. Most of these bones were unregistered but labelled 'Rodent Bed, Hordle Cliff, Hampshire'. The mammalian teeth (mainly rodent) have been separated from the rest of the debris, classified, and returned to the Sedgwick Museum. A few other boxes, only labelled 'Hordwell' contained fairly complete rodent maxillae and mandibles. The preservation, and adhering white sand matrix suggest derivation from the Mammal/Crocodile Bed; this material is not considered further in the present section. In a letter to Hinton, dated 22nd March 1932, Cooper remarked of the specimens he arranged to be borrowed by Hinton, '. . . some belong to the Sedgwick, some to me and one box to Watson'. This latter box, clearly marked 'property of D.M.S. Watson' has been returned to the University Museum of Zoology which now houses the Watson collection, but the specimens belonging to Cooper were not differentiated and have been returned to the Sedgwick Museum.

Screening of material at intervals along the outcrop has been carried out during recent fieldwork. Occasional rodent teeth and turtle fragments were recovered from the upper levels of the *Limnaea* Marl, and the overlying dark sandy clay has yielded a moderate quantity of small-sized vertebrate debris, including a few mammal teeth. The present rather unproductive nature of this horizon suggests that the

TABLE 1

Fauna of the Rodent Bed

		Numbers of specimens
Marsupialia:	'*Peratherium* species A'	2
Insectivora:	*Scraeva woodi* gen. et sp. nov.	1
	Heterohyus sp.	1
	Opsiclaenodon major	1
Primates:	*Microchoerus erinaceus*	4
Rodentia:	*Adelomys ?siderolithicus*	6
	Adelomys ?depereti	1
	Adelomys sp.	3
	Theridomyid spp.	519
Artiodactyla:	*Cebochoerus* sp.	1
	Dichodon cervinum	1

'Hinton loan collection', if indubitably from this level, was collected from a fossiliferous pocket which has been since exhausted.

A complete list of the known material from this horizon is given in table 1. This material is all of very small size and evidently represents a current-sorted accumulation; all the large Headon Beds species are absent. All the specimens are fragmentary and teeth are known only in the isolated state. Some of the material is water-worn. The sample is dominated by over 500 theridomyid teeth which may be referable to more than one species.

Depositional environment

In general aspect, the association of a dark coloured clayey sand with a comminuted shell bed is remarkably similar to associated dark clayey sands and comminuted shell beds which make up the Upper Headon *Microchoerus* Bed, discussed in detail in a later section. The depositional environment is probably closely similar, both associations representing shoreline deposits of muds, sands and shell banks. Evidently, mammalian material was carried onto this shore by a river or streams. The material was then broken up and size-sorted by strong current and wave activity, the small-sized fraction being eventually incorporated in the shoreline deposits.

Crocodile Bed

Stratigraphy

This horizon, about 2·1 metres of whitish sands, lies above the Leaf Bed and almost immediately below the upper ironstone band. It was first named as such in print by Wright in 1851. The upper part is made up of fine soft white sands but the lower layers are harder and brownish in colour. West of Hordle House, the bed outcrops at the base of the cliffs, rising westwards until west of Long Mead End, it is truncated by Plateau Gravels capping the cliffs.

Mammalian material apparently from this horizon was first described in 1844 and 1846 by Searles Wood, who recorded *Palaeotherium*, *Dichobune*, *Spalacodon* and *Microchoerus*. No precise level was given in this paper, but his son, Searles V. Wood, many years later verified that this material was obtained from the Crocodile Bed (Judd, 1882 : 475, footnote). The earliest reference to mammals being collected from the Crocodile Bed was by the Marchioness of Hastings (1848).

It appears that this horizon was first worked extensively by the Marchioness of Hastings, who recorded (1852 : 198) *Paloplotherium*, *Dichobune* and *Hyaenodon*: 'Parmi les mammifères nous avons: le *Paloplotherium;* une belle série de mâchoires et d'os est dans une collection . . . On y rencontre également le *Dichobune*, l'*Hyaenodon*. (J'ai dans ma collection une seule mâchoire inférieure parfaitement conservée . . .)'. She also listed crocodile material, several species of *Trionyx*, *Emys*, *Lepidosteus* and bird bones.

The Marchioness observed (1852 : 197) that abundant shells invariably accompanied the vertebrate remains and that the sand surrounding the bones ' . . . devient verdâtre, d'une nature boueuse ou argileuse, . . . '. She recorded that the most richly fossiliferous level was about three feet from the top of the bed and that the middle of the outcrop, a little to the west of Hordle House, was the most productive locality. It is evident from the Marchioness's account (1852 : 198) that most of the vertebrate remains were found closely packed together, in pockets which were widely separated and of infrequent occurrence: 'Les débris de *Lepidosteus* abondent dans cette couche, et se trouvent partout, mais en très grande quantité avec les os. Généralement la où se montrent les débris d'un animal, ou en trouve d'autres qui les accompagnent, et dans un espace de 6 verges on peut trouver des débris de toutes les espèces ci-dessus mentionées. . . . Après avoir trouvé un endroit fécond, il se peut qu'on explore des certaines de verges sans rien rencontrer que quelques coquilles, quelques écailles de poissons, des graines et des plaques osseuses de peau de crocodile, débris qui sont très abondants.'

The Marchioness described one such pocket in her earliest account of the Hordle cliffs (1848 : 63): ' . . . the vertebrae and other bones of the Crocodile and Paloplotherium were found at intervals of from four inches to three feet apart to the westward of the heads . . . I must not omit likewise to state, that close to this crocodile's head (the whole group comprising a space of about six feet long by ten inches only in thickness, and following each other nearly in a straight line) were found the nearly entire shell of a fossil Trionyx . . . and the jaw, vertebrae, and scales of a fish of the order *Lepidosteus*.'

It is likely that a large part of the early museum collections came from these richly fossiliferous pockets in the Crocodile Bed which were largely worked out by the Marchioness of Hastings. As far as is known, no important mammalian material has been recorded subsequently from this horizon. Recent examination has produced only scales of *Lepisosteus* and occasional crocodile and turtle bones.

Depositional environment

No detailed examination of this horizon has been undertaken. Dr N. Edwards who has been working on the sedimentation of the Headon Beds considers (personal communication) that the Crocodile Bed was deposited near the mouth of a river. This river, inhabited by turtles, crocodiles and fish, brought in mammalian material and large quantities of detrital sediments. Estuarine elements in the molluscan fauna indicate a slight saline influence. The rich pockets of vertebrate remains worked by the Marchioness of Hastings, may have accumulated in scour channels between sand bars.

Mammal Bed

Stratigraphy

This horizon, bed No. 9 of Tawney & Keeping, comprises about 3·7 metres of bluish-green clays, white-brown sands and blue sandy clays, occurring between the Leaf Bed and the lower ironstone band. It outcrops at the base of the cliffs just west of Hordle House, running westwards to Becton Bunny, where at the top of the cliffs it is overlain by Plateau Gravel.

The first reference to mammalian material from this horizon may have been by Owen (1846 : 323) who recorded a fragmentary humerus and a lower molar of *Palaeotherium* 'from the Eocene clay at Hordwell'. Two years later, Owen (1848) described *Palaeotherium medium, Paloplotherium annectens* and *Dichodon cuspidatus* obtained by Falconer 'from the Eocene Sand at Hordle, Hampshire'. Although Wright (1851) stated (without giving reasons) that these specimens came from the Mammal Bed, it appears, from the accounts of the Marchioness of Hastings (1848; 1852) and Owen (1848), that some of the material was derived from the Crocodile Bed.

The Marchioness of Hastings (1852) described the Mammal Bed in detail, listing vertebrate material from the various subdivisions, although no precise localities were given. At the top, just below the Leaf Bed, the Marchioness recorded a green clay containing mammalian material. She stated (1852 : 200), 'J'ai une mâchoire inférieure très écrasée (comme tous les débris qu'on trouve dans cette partie) d'*Anthracotherium*, et probablement des portions de mâchoire inférieure de *Paloplotherium*.'

Below this clay, the Marchioness mentioned white sands containing several thin ironstone bands; the sands contained, associated with layers of shells, well preserved vertebrate remains which were not common, and were difficult to extract. She recorded, ' . . . on trouve des *Trionyx*, des *Emys*, des fragments de mâchoires des mammifères, avec des dents, des vertèbres de poissons, parfois des os, des ossements d'oiseaux, et de très petites mâchoires, mais pas de crocodiles'.

The next well-defined horizon recorded by the Marchioness was a bed of whitish-brown sand with bands of green clay in places. The upper half of this bed contained the same vertebrate material as that from the overlying bed.

The best specimens were obtained from the lowest part of the Mammal Bed—bluish-green sandy clays. The Marchioness stated (1852 : 201), 'J'ai tiré de là une dent d'*Anoplotherium* commun et une *scapula, 2 tibias, 2 Humérus, Métacarpes*, etc, qui sont indéterminés, mais que je crois d'*Anoplotherium*, des *Paloplotherium*, des débris de *Crocodile*, des Trionyx, des oiseaux, un très grand poisson inconnu, des Emys.'

Subsequently, the Mammal Bed has apparently yielded little material. Tawney & Keeping (1883) observed of this horizon, 'We had the good fortune to find the mandible of a *Dichodon* here on our last visit. Mammals, however, have been seldom found of late years'. A fragmentary mandible, the type of '*Hyaenodon aimi*', was discovered in 1926. No precise locality was recorded, but the specimen, according to Mr F. C. Stinton (personal communication), came from the Mammal Bed at Long Mead End. Examination of this horizon in 1961 and 1962, yielded only a single ungulate calcaneum; this came from slumped debris at Long Mead End.

Depositional environment

Dr N. Edwards has suggested (personal communication) that the Mammal Bed generally, was laid down in 'coastal fen-land waters' and probably represents various stages in a silting-up cycle from shore conditions (Long Mead End sands at the top of the Barton Beds) to swamp (Leaf Bed).

Mammalian fauna of the Mammal/Crocodile Bed

A combined list of all the mammalian material which has probably been derived from the Mammal Bed and Crocodile Bed is given in Table 2.

Table 2

Fauna of the Mammal/Crocodile Bed

		Numbers of specimens
Marsupialia:	'*Peratherium* species A'	6
	'*Peratherium* species B'	4
Insectivora:	*Scraeva woodi* gen. et sp. nov.	4
	Opsiclaenodon major	21
Primates:	*Adapis magnus*	51
	Microchoerus erinaceus	45
	Pseudoloris parvulus	1
Rodentia:	*Adelomys ?depereti*	1
	Adelomys sp.	1
	Theridomyid spp.	176
Creodonta:	*Hyaenodon* c.f. *minor*	10
Carnivora:	*Quercygale hastingsiae*	1
Perissodactyla:	?*Anchilophus* sp.	2
	Plagiolophus annectens	33
	Plagiolophus minor	11
	Palaeotherium muehlbergi praecursum	6
	Palaeotherium sp.	7
Artiodactyla:	*Cebochoerus* sp.	1
	Choeropotamus depereti	1
	Dacrytherium ovinum	1
	Catodontherium sp.	2
	Haplobunodon lydekkeri	3
	Haplobunodon sp.	1
	Anthracotheroid *incertae sedis*	1
	Dichodon cuspidatus	30
	Dichodon cervinum	3
	Pseudamphimeryx hantonensis	2

Some of the material was apparently associated. Representatives of all orders, a total of 28 species, are present, of which one third are known only by single specimens; this is the most complete sample known from the Headon Beds, but as noted earlier, the material was probably collected from several distinct lithologies within a vertical interval of about 9 metres.

As with the Rodent Bed, the sample is dominated by rodents, mainly theridomyids, which make up a little under half of the sample. Primates are next in abundance, representing just under one quarter of the sample. Perissodactyls are slightly more abundant than artiodactyls, the specimens of the two orders combining to form about one quarter of the sample. The Artiodactyla show the most diversity: 10 species are present of which 5 are represented by single specimens. Insectivores, marsupials, creodonts and carnivores, in order of decreasing abundance, make up only a small fraction of the sample.

Minor horizons

Green clay (2·7 metres) below the Unio Bed

This horizon, numbered 30 by Tawney & Keeping (1883) corresponds in part, according to these authors, to bed 4 of the Marchioness of Hastings. The Marchioness mentioned small undescribed teeth and jaws of mammals obtained from sandy partings in these green clays. She stated (1852 : 195), 'Les lignes sablonneuses contiennent des *Paludina lenta*, des *Potamomya plana*, très pressées, des débris de poissons, des vertèbres et des écailles, de petites dents de *mammifères* non décrits, avec de très petites mâchoires. J'ai un grand *calcaneum* trouvé dans cette couche: c'est le seul grand os qu'on y ait jamais rencontré.'

An isolated theridomyid upper incisor, part of the Hinton loan of Hordle rodent material, is labelled '6 feet below *Limnocarpus* Bed'. The term '*Limnocarpus* Band' was first applied by Chandler (1922 : 224) to a thin bed rich in seeds of *Limnocarpus*, situated near the base of the *Unio* Bed. As the *Unio* Bed (Bed 31 of Tawney & Keeping, 1883) is about 2·4 metres thick, this tooth probably came from the green clays below, close to the Marchioness's original horizon.

Rolled-bone Bed

This horizon, so named by Tawney & Keeping (1883) because of the worn appearance of its vertebrate content, was listed by them as bed No. 13. This apparently corresponds to part of the Marchioness's bed No. 11. It is composed of 0·15–0·23 metres of greyish-white sands, occurring just below the base of the Crocodile Bed.

The Marchioness of Hastings recorded worn bones of rodents and other mammals from this horizon. In 1852 (p. 199) she wrote, ' . . . ; on y trouve aussi en assez grande abondance des os roulés d'*Emys*, de *Trionyx*, *Crocodile*, *Rongeurs*, des vertèbres de poissons, d'oiseaux et de mammifères.' She observed that the best preserved specimens were mammalian teeth which were sometimes nearly intact; the rest of the material was rounded and hardly recognisable.

Whitish sand above the Leaf Bed

The Leaf Bed, numbered 10 by Tawney & Keeping, is a plant-bearing carbonaceous clay, 0·23–0·46 metres thick, occurring between the Crocodile Bed and the Mammal Bed. Immediately overlying this Leaf Bed, is a whitish sand (No. 11 of Tawney & Keepings' account), from the base of which, the Marchioness of Hastings recorded an associated group of palaeotheroid bones. She stated (1852 : 199), ' . . . , à la base de la couche, et près de son extrémité, on a trouvé dans l'espace de quelques verges environ 30 os, appartenant évidemment au même animal, un *Palaeotheroide*.'

Thin shell bed above the Lower Ironstone Band

This horizon occurs immediately above the ironstone band (numbered 8 in Tawney & Keepings' section), which is usually considered to mark the base of the Mammal

Bed. It is included here as a distinct horizon, because it has been so well defined by the Marchioness of Hastings and its mammalian content is very similar to that of a bed below the ironstone band (see below). Amongst the vertebrate material obtained from this horizon, the Marchioness (1852 : 201) listed mammalian teeth and rodent jaws: 'On y trouve également des vertèbres de serpents et de lézards, des dents de mammifères, des mâchoires de rongeurs, des écailles et des vertèbres de poissons, des débris de crocodiles, de *Trionyx* et d'*Emys*, et parfois des os plus gros et même conservés, comme des astragales et des os du carpe.'

Thin white sandy marl below the Lower Ironstone Band

This was listed by Tawney & Keeping as bed No. 7 and was stated by them to be 1 inch thick. The Marchioness mentioned that this bed contained about the same vertebrate material as that recorded from the horizon immediately above the ironstone.

(c) Horizons at Headon Hill, Isle of Wight

(i) Introduction

The Reading Beds-Barton Clay are traditionally considered as being in Alum Bay, and the Headon Hill Sands (Barton Sands) and higher beds are referred to Headon Hill, although the section is continuous.

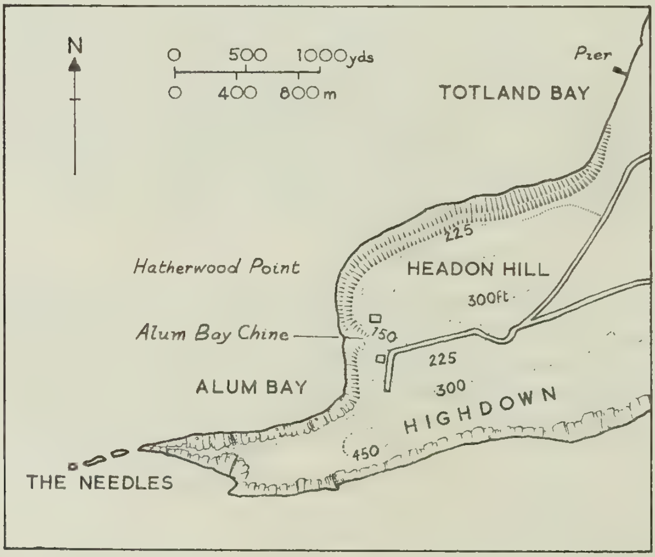
N
0 500 1000yds
0 400 800m
Pier
TOTLAND BAY
225
Hatherwood Point
HEADON HILL
300ft
Alum Bay Chine
150
225
300
ALUM BAY
HIGHDOWN
450
THE NEEDLES

FIG. 5. Locality map of Alum Bay and Headon Hill, Isle of Wight.

Alum Bay is bounded to the south by the almost vertical Chalk ridge of High Down which terminates westwards in the Needles. The Reading Beds-Barton Clay are almost vertical, but in the upper part of the Barton Clay and in the overlying Headon Hill Sands situated immediately north of the mouth of Alum Bay Chine, the dip changes rapidly (in less than one hundred metres laterally) from vertical to horizontal (figs 5 and 6). The seaward face of Headon Hill is composed of the overlying nearly horizontal Headon and Osborne Beds, forming the lower limb of the monocline. The summit of the Hill is capped by Plateau Gravel.

The soft sands and clays of the vertical Alum Bay section form a high very steep sea cliff which is retreating rapidly due to natural erosion and the activities of coloured-sand collectors. By contrast, the seaward face of Headon Hill is relatively more gently inclined, receding inland to the summit of the hill as a series of inclined 'steps'. These 'steps', caused by the erosion of soft sands and clays occurring between bands of limestone, are usually covered by thick scree and mud-flow deposits, and often support a partial cover of vegetation. As a result, exposures here are usually discontinuous and short-lived. The relatively more resistant limestone bands stand out as scar-like cliffs in the side of the hill. The highest of these cliffs is formed by the limestone in the Osborne Beds (near the middle of the Osborne Beds); the middle cliff by the Upper Headon Limestone (at the base of the Upper Headon Beds), and the lowest and smallest cliff by the How Ledge Limestone (at the top of the Lower Headon Beds). A generalised section of the Headon Beds at the south-west corner of Headon Hill, is given in fig. 7.

By comparison with Hordle Cliff, little mammalian material has come from the Headon Hill horizons. Until recently, a jaw of *Dichodon* was the only recorded specimen (Wright, 1851a, 1852) from the Lower Headon Beds in this area. The only precise reference to mammalian material from the Upper Headon Beds of Headon Hill, was by Prestwich (1846) who listed bones and teeth of *Palaeotherium* from the Upper Headon Limestone above and below the Lignite Bed; these specimens are apparently lost.

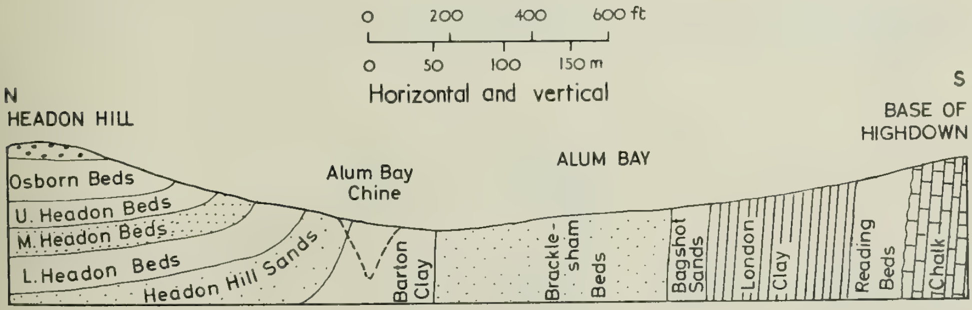

FIG. 6. Cliff section at Alum Bay and Headon Hill, Isle of Wight, showing the Reading Beds—Headon Beds. Based on Curry, 1958c, fig. 2.

Several museum specimens of *Dichodon*, *Haplobunodon* and a theridomyid are labelled 'Isle of Wight' or 'Eocene? North-west coast of the Isle of Wight', and Lydekker (1885c) listed *Dichodon* and *Dacrytherium* specimens from the 'Headon Beds, Isle of Wight'. White sand matrix adhering to some specimens, and the

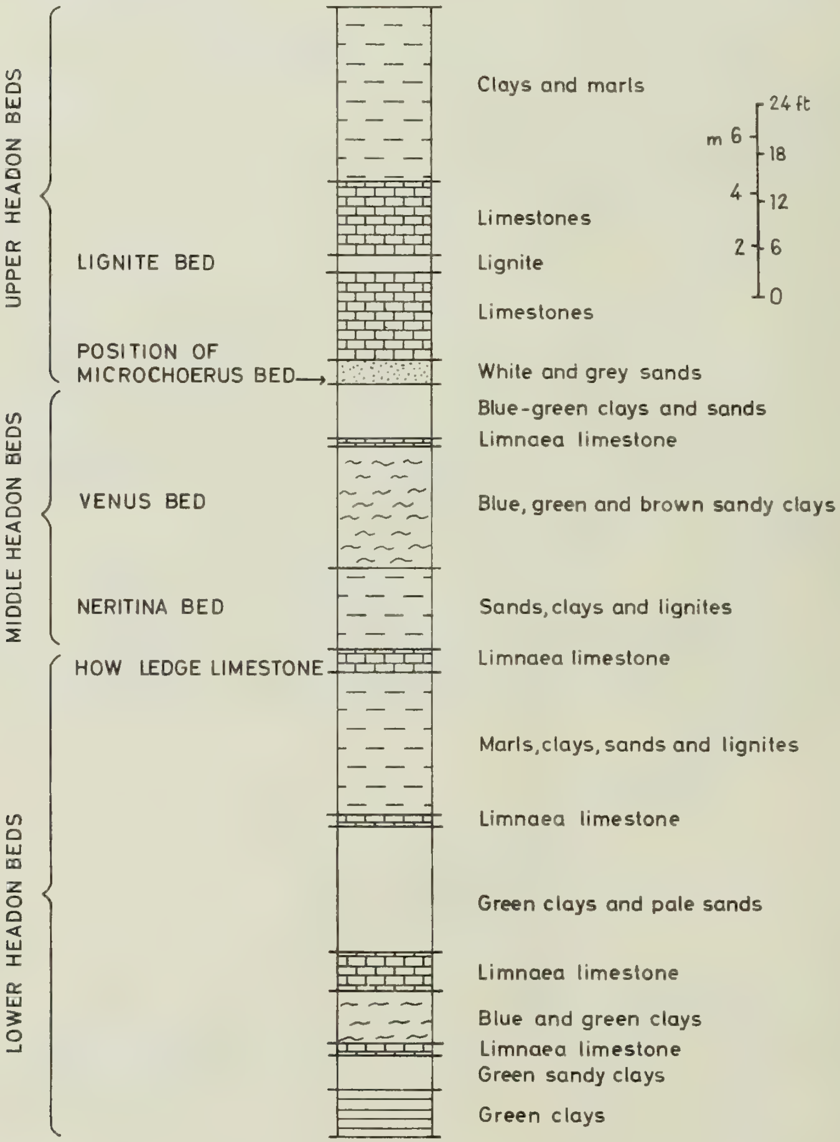
UPPER HEADON BEDS
MIDDLE HEADON BEDS
LOWER HEADON BEDS
LIGNITE BED
POSITION OF MICROCHOERUS BED
VENUS BED
NERITINA BED
HOW LEDGE LIMESTONE
Clays and marls
Limestones
Lignite
Limestones
White and grey sands
Blue-green clays and sands
Limnaea limestone
Blue, green and brown sandy clays
Sands, clays and lignites
Limnaea limestone
Marls, clays, sands and lignites
Limnaea limestone
Green clays and pale sands
Limnaea limestone
Blue and green clays
Limnaea limestone
Green sandy clays
Green clays
m 6
4
2
24 ft
18
12
6
0

FIG. 7. Generalized succession of the Headon Beds at the south-west corner of Headon Hill, Isle of Wight.

above information from museum labels or Lydekker's Catalogue, point to derivation from the Lower Headon Beds. Two unlabelled theridomyid teeth have an adhering matrix of soft marly limestone, suggesting a probable derivation from either the Upper Headon Limestone or the Lower Headon How Ledge Limestone of Headon Hill. As the precise horizons of all this material are not known with certainty, the specimens are not included in the faunal lists.

One specimen, a palatal fragment of *Palaeotherium*, although listed by Lydekker (1886) as 'from the Isle of Wight. No history' is embedded in a shelly lignite with an associated soft shelly limestone; this matrix strongly suggests derivation from the Upper Headon Lignite Bed. Owing to the distinctive lithology of the matrix, this conclusion is considered reliable and the specimen is included in the faunal lists, constituting an isolated early record from the Lignite Bed.

In the last few years, further mammalian material has been obtained from the Lignite Bed in moderate quantity and a new mammal-yielding horizon below this, at the base of the Upper Headon Beds, has been discovered during recent fieldwork. In 1961, a mammal-bearing horizon was found near the top of the Lower Headon Beds.

Recorded below are all the definite mammal-yielding localities at Headon Hill, together with lists of mammalian material collected from them.

(ii) Lower Headon Beds

Minor horizons

Green clay, 2·1 metres above the top of the Headon Hill Sands

This horizon, recorded by Wright (1851 : 25 and 1852 : 87), yielded one specimen, a fragmentary mandibular ramus of *Dichodon cuspidatus*. Recent examination of this bed at the south-west corner of Headon Hill, has not produced further material.

Green marl immediately below the How Ledge Limestone

The post-cranial skeleton of a small mammal was obtained recently by Dr N. Edwards from this horizon at the south-west corner of Headon Hill. The specimen has not yet been described.

(iii) Upper Headon Beds

Microchoerus Bed

Stratigraphy

The *Microchoerus* Bed, named from the first mammal found, is a small lenticular horizon at the junction of the marine Middle Headon Beds and the freshwater Upper Headon Beds, at the south-west corner of Headon Hill. The lateral extent of this lens, which outcrops along the base of the Upper Headon Limestone cliff, is about 100 m (fig. 8).

A section through the thickest development (about 0·33 m) shows:

Purple and grey clay Purple clayey sand	0·10 m
Comminuted shell bed	0·15 m
Buff clayey sand	0·08 m

The *Microchoerus* Bed is overlain by white unfossiliferous sands, generally considered of Upper Headon age. The lowest part of the *Microchoerus* Bed, a buff clayey sand, rests abruptly on a comminuted shell bed which grades down vertically and passes laterally into a shelly blue-green clay. The shell bed and shelly clay both contain a marine fauna, including foraminiferida, and thus are best considered as Middle Headon in age. The *Microchoerus* Bed containing terrestrial detritus, forms a fairly distinct unit which is referred to the Upper Headon Beds.

The buff clayey sand, containing wood fragments and mammalian material, lies on an irregular upper surface of the lower comminuted shell bed. The upper surface of the buff clayey sand is irregular and in places, strongly fissured. The comminuted shell bed is composed mainly of fragments of lamellibranchs (?*Corbicula obovata, Sinodia suborbicularis*) with a few gastropod fragments (*Batillaria concava*). The bed is very lenticular, infilling hollows in the underlying sand; occasionally it is completely absent. In places, small lenses of sand are incorporated in the base. The purple sand and clay, containing mammalian material and wood fragments,

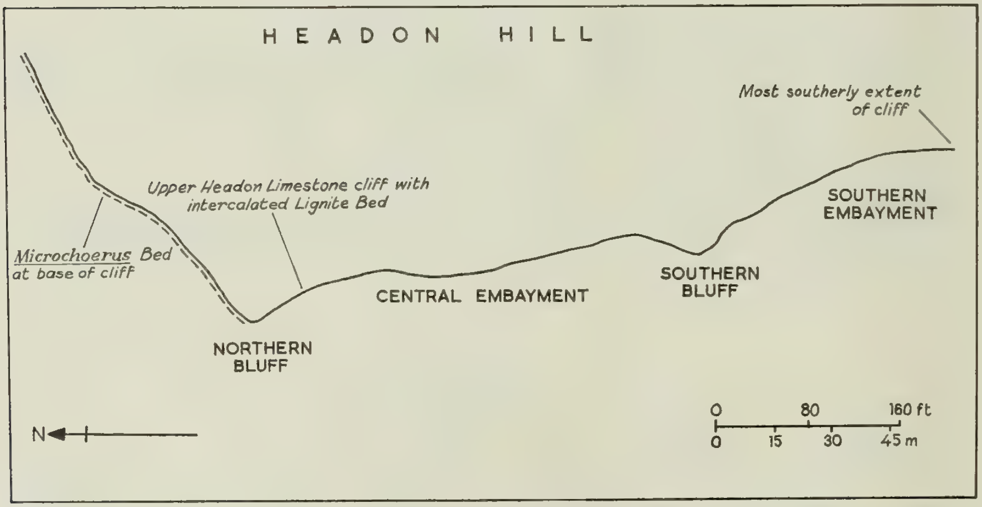
HEADON HILL
Most southerly extent of cliff
Upper Headon Limestone cliff with intercalated Lignite Bed
SOUTHERN EMBAYMENT
Microchoerus Bed at base of cliff
SOUTHERN BLUFF
CENTRAL EMBAYMENT
NORTHERN BLUFF
N
0 80 160 ft
0 15 30 45 m

FIG. 8. Map showing location of the *Microchoerus* Bed and Lignite Bed at Headon Hill, Isle of Wight. Based on a plan of the top of the Upper Headon Limestone cliff, at its most southerly outcrop on Headon Hill.

infills irregularities in the underlying shell bed. Where the latter is absent, it directly overlies the buff sand; here, shell material and lenses of buff sand are incorporated in the base of the purple sand.

Mammalian fauna

During 1962, attention was focussed on the *Microchoerus* Bed by the discovery of fragmentary mandibles of *Microchoerus* and *Scraeva* gen. nov. in the intermixed purple and buff clayey sand in the northern part of the outcrop.

The following summer, excavations were made at intervals along this part of the outcrop. About 12 m laterally was exposed and examined by handpicking and screening of the residues. Unfortunately this horizon could be followed back into the cliff for only one metre; extensive white sand overburden and overhanging limestone made further development impracticable. A badly crushed fragmentary mandible of *Catodontherium* was discovered in the iron-stained lower part of the white sand immediately overlying the *Microchoerus* Bed. A fragmentary mandibular ramus of *Peratherium* was one of several specimens obtained from a pocket of the buff clayey sand; it was badly crushed and had lost all teeth except M_3, presumably during transport. The root tips of this tooth were just lodged in the alveoli, the displacement being evidently a result of final impact with the substratum before burial. The intermixed purple and buff clayey sand yield 12 isolated, randomly orientated upper teeth of a palaeothere, ?*Palaeotherium muehlbergi praecursum*. These teeth with parts of the maxillae and palate were spread over about 0·30 m. It is likely that the strong current activity during the deposition of the purple clayey sand caused fragmentation of the original palatal specimen.

TABLE 3

Fauna of the *Microchoerus* Bed

		Numbers of specimens
Marsupialia:	'*Peratherium* species A'	1
Insectivora:	*Scraeva hatherwoodensis* gen. et sp. nov.	1
Primates:	*Microchoerus erinaceus*	1
Rodentia:	Theridomyid sp.	6
Perissodactyla:	?*Palaeotherium muehlbergi praecursum*	1
Artiodactyla:	*Catodontherium* sp.	1

A list of all material obtained from this horizon is given in Table 3. This sample is incomplete both in numbers of species and frequency of individuals. Creodonts and carnivores are absent; all other orders, except the rodents, are known only by single specimens. This is probably largely due to incomplete sampling, but as most of the specimens are of small size, is probably also affected by preferential current-sorting.

Depositional environment

The *Microchoerus* Bed evidently represents shoreline deposits left behind by the retreating Middle Headon Sea. Limited evidence from the deposition of the various individual beds in the northern part of the outcrop, suggests that the present-day cliff section represents an approximate cross section through this shoreline which trended roughly east-south-east to west-north-west. Terrestrial detritus such as wood and vertebrate remains (mainly mammalian) was carried into the brackish sea by streams to be incorporated in the shore deposits. Possibly at low water, these deposits were exposed on the foreshore as irregular spreads of mud and sand which occasionally dried out forming shrinkage cracks in the upper layers. Through strong wave activity, irregular spreads of comminuted shells accumulated in places as lenticular shell banks. General intermixing of sediments, balled-up clay pellets, scoured surfaces and broken-up mammalian remains, all testify to the erosive effect of strong current activity during the deposition of most of the *Microchoerus* Bed.

Lignite Bed

Stratigraphy

This horizon occurs within the Upper Headon Limestone, outcropping about a third of the way up the vertical cliff formed by the limestone on the south-west seaward face of Headon Hill; the lignite mainly infills an irregular erosion surface in the underlying limestone. Where the Lignite Bed is well developed, it is affected by small-scale block faulting and other post-depositional compaction phenomena.

The position of the main outcrop of the Lignite Bed is indicated on a plan showing the top of the Upper Headon Limestone cliff as it appeared in 1963 (fig. 8). At the most southerly extent of this cliff, just north of Alum Bay Chine, the beds dip northwards at about 40° as they become involved in the middle limb of the main Isle of Wight monocline; further north the beds are approximately horizontal.

The Lignite Bed and associated limestones were described by Jackson (1924). In earlier stratigraphical accounts, the bed had been largely unnoticed; it was mentioned by Judd (1880) and Lee (1881). This was accounted for by Jackson who suggested (1924 : 278) that as the deposits appear to thin towards the face of the cliff 'hence they were probably less conspicuous in times past'. This view is supported to some extent by the present distribution of the Lignite Bed: where the limestone cliff at present forms projecting bluffs, the lignite is very thin or absent, and the thickest development is in the intervening embayments.

In many places the Lignite Bed is intimately associated with the underlying limestone; this limestone is very variable lithologically and several subdivisions were recognised by Jackson (1924). The commonest type (this overlies the Lignite Bed also) is a soft impure orange marly limestone with abundant shalls of *Galba* spp. and *Planorbina* spp., fragments of turtle bones and more rarely, fragmentary mammalian remains.

A general section through the thickest development of the Lignite Bed in the southern embayment is as follows:

Lignitic shell marl	0·23 m
Hard black carbonaceous clay	0·15 m

The carbonaceous clay contains seams of shell debris and infills irregular curved fissures in the underlying marl, which often penetrate the marl to a depth of 0·61 m. The overlying lignitic shell marl is made up of comminuted shells (*Galba* spp. and *Planorbina* spp.) with thin partings of friable lignite. In the extreme south, no erosion surface is evident and the lower marly limestone passes up through a thin shell marl (representing the Lignite Bed) into the upper marly limestone.

In the central embayment, the Lignite Bed consists of the following:

Friable black lignite	0·08 m
Laminated lignitic shell marl	0·15 m
Friable black/brown lignite	0·43 m

The friable black/brown lignite in many places infills solution channels excavated usually in the soft underlying marly limestone; hard white nodular limestone bands often project into the lignite as isolated residual solutioned blocks. These solution channels are up to 0·30 m deep and appear to trend north-west to south-east. Occasional lignite-filled fissures penetrate deeply into the marl (up to 1·2 m in the northern part of the embayment). The overlying lignitic shell marl probably corresponds to the lignitic shell marl of the southern embayment; it contains several partings of friable lignite, two of which form distinct bands. This shell marl rests directly on a smooth solutioned surface of hard limestone at the southern bluff. Near the northern bluff, a shelly black lignitic clay infills smooth funnel-like sub-horizontal potholes in the underlying hard rubbly and marly limestones; these potholes trend north-south. In this area, several minor lignitic lenses occur in the limestones above and below the main Lignite Bed. At the northern bluff, the upper and lower limestones are only separated by an undulating erosion surface and the Lignite Bed has largely disappeared. Further north of this, the horizon either persists as a thin lignitic shell bed or its position is indicated by an erosion surface.

Throughout the Lignite Bed, the beds of shell marl and lenses of shell debris are made up mainly of flattened *Galba* spp. and *Planorbina* spp. Isolated crocodile teeth (*Diplocynodon* sp.) and dermal scutes and other bones of turtles (*Emys* sp.) occur sporadically throughout the horizon, both in the friable lignite and the shell marls. One small badly preserved jaw fragment, ?fish, was obtained from the top friable lignite in the southern part of the outcrop. Samples of lignite were sent to Dr J. M. Pallot for pollen analysis; pollen was identified only from a restricted range of woodland trees: *Pinus, Myrica* and *Engelhardtia* (personal communication).

Depositional environment

The previously described *Microchoerus* Bed apparently represents shoreline deposits left behind by a receding Middle Headon sea. After this regression, freshwater lagoonal conditions prevailed in the area, with extensive terrestrial detritus, including mammalian remains, being supplied by some fluviatile agency. Initially, sand was carried into these lagoons and spread over the abandoned muds, sands and shell banks of the retreating sea. This was soon followed by extensive carbonate deposition. The waters of the lagoons were colonised by molluscs, crocodiles and turtles;

at times growth of algae took place. Breccias, conglomerates, nodular and rubbly limestones indicate extensive penecontemporaneous erosion during the carbonate deposition. With shifting of these waters, parts of the lagoonal floor became exposed at times, drying of the sediments causing the formation of deep shrinkage fissures; elsewhere, the surface became trenched with a system of terrestrial streams which scoured out deep channels in the soft semi-consolidated marl. Hollows, potholes, and rounded surfaces were formed in the harder limestone bands by solutioning. The agency of terrestrial stream erosion was first suggested by Jackson (1924 : 278). The erosion of about 1 m of lagoonal sediments resulted in the formation of hollows, e.g. at the present-day central embayment. The southern part of the area may have been covered by shallow lagoonal waters for most of this time.

With the return of lagoonal conditions, considerable quantities of woodland vegetation were carried into these erosion hollows, to accumulate first in the fissures and scour channels. At times there were influxes of fine detrital material, resulting in the accumulation of carbonaceous muds. Periodically spreads of shells were concentrated by current activity and incorporated amongst the vegetable debris.

Mammalian fauna

With the exceptions of one specimen recorded by Lydekker (1886) and the unlocated specimens listed earlier by Prestwich (1846), all the material has been collected within the last decade. Jackson (1924) recorded the complete absence of vertebrate material.

This horizon was first examined by the author in 1961. In the following two years, a series of excavations were made at intervals along the outcrop of the Lignite Bed. About 9 m laterally was examined in this way but because of the intercalation of the lignite between relatively hard limestones, the bed could only be followed into the cliff for about 1m.

Some interesting, though not very abundant material was found: in the northern part of the main outcrop, two associated lower teeth of *Dyspterna hopwoodi* sp. nov. were obtained from a thin friable lignite overlying infilled solution hollows. The thick development of the lignite in the central part of the outcrop yielded several partially-associated long bones and a scapula, probably of a palaeothere. These bones, from the uppermost friable lignite, were fragmentary, randomly-orientated and much decomposed; they occurred within an area of about 1 m and almost certainly belonged to a single individual. At the same locality, a mandible of *Dyspterna hopwoodi* sp. nov. was found in the underlying main lignitic shell marl. Several associated upper teeth of *Palaeotherium* were discovered in the lowermost black friable lignite in the same area. Three of these teeth (P^1–P^3) were closely associated with the powdery remains of bone fragments; an isolated M^3 from about 0·15 m away, probably belonged to the same individual.

A complete list of the mammalian fauna from this horizon (and associated limestones) is presented in Table 4. The species list is more extensive than that of the *Microchoerus* Bed and all orders except the Creodonta and Marsupialia are represented by more than one species. The sample is incomplete, and the frequency of individuals is very low, most species being represented only by single specimens.

TABLE 4

Fauna of the Lignite Bed

		Numbers of specimens
Marsupialia:	'*Peratherium* species A'	1
Insectivora:	*Arvaldus stintoni* gen. et sp. nov.	1
	Dyspterna hopwoodi sp. nov.	3
Primates:	*Adapis parisiensis*	1
	Microchoerus erinaceus	1
Rodentia:	*Adelomys siderolithicus*	1
	Theridomyid sp.	7
Creodonta:	*Hyaenodon* c.f. *minor*	1
Perissodactyla:	*Plagiolophus annectens*	1
	Palaeotherium muehlbergi muehlbergi	1
	Palaeotherium muehlbergi praecursum	5
	Palaeotherium sp.	1
Artiodactyla:	*Dichodon cuspidatus*	1
	Haplobunodon lydekkeri	1

Much of the small material was collected by Mr F. C. Stinton by screening the main lignitic shell bed (personal communication); these specimens probably represent a current-sorted accumulation. With the other larger-sized material from the friable brown lignite and the black shelly lignitic clay, no current sorting is evident, and the partially-associated bones probably indicate more tranquil conditions of deposition.

Mammalian material is consistently but sparsely distributed throughout the Lignite Bed and processing of a large volume of sediment is necessary to obtain an adequate sample. As the bed outcrops in a vertical cliff, intercalated between relatively hard limestones, extensive working of this horizon is rendered difficult. In spite of these practical difficulties, the Lignite Bed remains potentially one of the most favourable sites for further development.

III. SYSTEMATIC DESCRIPTIONS

Order MARSUPIALIA

Family **DIDELPHIDAE** Gray, 1821

DIAGNOSIS. Small polyprotodont marsupials. Dental formula $\frac{5-?}{4-3}$, $\frac{1}{1}$, $\frac{3}{3}$, $\frac{4}{4}$. Incisors all small. Canines large. Premolars simple, trenchant or bulbous. Lower molars tuberculo-sectorial with three trigonid cusps and basined heels with hypoconulid postero-internal, near entoconid. Upper molars trigonal, with no true hypocone, external cingulum wide, with various well-defined marginal cusps (styles). Quadrupedal, plantigrade, usually with opposable hallux and pollex, often with prehensile tail (from Simpson, 1929, and 1935a : 136).

REMARKS. The generally accepted subdivision of the family is that of Simpson (1935a). Four subfamilies are recognised: Pediomyinae Simpson, 1927; Thlaeodontinae Hay, 1930; Microbiotheriinae Simpson, 1929 and Didelphinae Simpson, 1927.

Subfamily **DIDELPHINAE** Simpson, 1927

DIAGNOSIS. Premolars trenchant. Paracone much reduced, except on M^4. Marked metastylar spur. Style B large, D smaller than C. Paraconule reduced or absent (modified from Simpson, 1935 ; 137).

REMARKS. Distinguished from the other subfamilies as follows: In the Microbiotheriinae, the styles are weak and there is no distinct metastylar spur; M_4 is reduced and more simple. The Thlaeodontinae have bulbous crushing premolars; the paracone and metacone are subequal and there is no distinct metastylar spur. In the Pediomyinae, the paracone and metacone are subequal; style B is weak with D larger than C, and there is a definite paraconule.

The Didelphinae ranges from the Early Palaeocene—Early Miocene of North America; ?Palaeocene, Early Eocene—Miocene of Europe; Pliocene—Recent of South America and Pleistocene—Recent of North America. The genera currently grouped in the subfamily are as listed by Simpson (1945) with the addition of two North American forms: *Herpetotherium* Cope, 1873, from the Early/Middle Oligocene and *Didelphidectes* Hough, 1961, from the Early Oligocene.

The structure of the lower molars in didelphines is remarkably uniform and on this basis, early Tertiary forms can barely be distinguished from the living representatives of the group, the American opossums. Unfortunately, most fossil didelphines are known from fragmentary mandibles and satisfactory generic separation is difficult; the subfamily clearly needs a thorough revision.

Genus ***PERATHERIUM*** Aymard, 1850

TYPE SPECIES. *Peratherium crassum* (Aymard, 1846). Early Oligocene ('Sannoisian') Ronzon, France. The specimen is apparently lost.

REMARKS. The genus *Peratherium* is known from the Eocene—Miocene of Europe and North America; it is the only fossil didelphine genus recorded from Europe.

Hough (1961 : 221) revived Cope's genus *Herpetotherium*, to receive certain American species, previously described as '*Peratherium*', having an uninflected angular process. The remaining American species of *Peratherium* (with inflected angulars) appear to be generically indistinguishable, on the basis of lower dentitions, from the European material and from living representatives. However, the extensive range and geographical distribution of this genus, make it likely that a better knowledge of the upper dentition of these forms will reveal several distinct genera.

About 30 species are described from Europe and about 12 from North America. Most of the European species (recently listed in Quinet & Misonne, 1967 : 5) are based on mandibular fragments, but several of the American forms are known only from upper dentitions. Of the European species, only about half of the types have been located in various museums. Many of the early types of species erected by Filhol, Blainville, Aymard and Gervais apparently are lost and the original figures and descriptions are now inadequate for detailed comparison. Examination of recent didelphid material (Hough, 1961 : 219) reveals much individual variation, together with sex and age differences within a single species. Undoubtedly, many European species distinguished mainly on size are invalid. Crochet (1969) recognised four European species of *Peratherium* of which two, *P. laurillardi* Gervais, 1848–52 and *P. cuvieri* Fischer, 1829, are known from the Ludian.

As the genus *Peratherium* is being revised by Herr W. v. Koenigswald at München[1], no diagnoses are given here; the Headon Beds material is designated merely as '*Peratherium* species A' and '*Peratherium* species B'.

'***Peratherium*** species A'

(Text-figs 9–11)

Material. All specimens from the Lower Headon Beds (Mammal/Crocodile Bed), Hordle Cliff, except where otherwise stated.

B.M. 30350. Fragment of right mandibular ramus with M_2–M_4. The angular process and the basal part of the coronoid are preserved.

S.M. C30707. Fragment of right mandibular ramus with P_2–M_4, and alveoli of I_1–P_1. Symphysis is preserved. Associated posterior region of mandible almost complete—from same individual?

S.M. C30708. Fragment of left mandibular ramus with M_3 and parts of alveoli of M_2 and M_4.

S.M. C53476. Fragment of left mandibular ramus with M_2–M_3 and alveoli of M_4. Base of coronoid preserved.

B.M. 36812b. Isolated right M_4. Unworn.

B.M. 30348. Fragment of right mandibular ramus with M_3–M_4 and alveoli of P_2–M_2. Teeth well worn.

B.M. M26050. Fragment of right mandibular ramus with M_3. The tips of the roots just rest in the alveoli. Upper Headon Beds (*Microchoerus* Bed), Headon Hill.

F.C.S. 2. Isolated right M_3. Upper Headon Beds (Lignite Bed), Headon Hill.

S.M. C54170. Isolated left M^2. Fairly well worn. Lower Headon Beds (Rodent Bed), Hordle Cliff.

S.M. C54171. Isolated left M^3. Almost unworn. Lower Headon Beds (Rodent Bed), Hordle Cliff.

Description. In S.M. C30707, the jaw is long and slender. The posterior mental foramen lies below M_1 and the anterior mental foramen below P_2. The subhorizontal symphysial surface occupies only the basal half of the mandible; it has a ridged upper margin and extends posteriorly to below P_2. Two internally-situated nutrient foramina are visible: the larger foramen opens through the symphysial surface into the posterior part of the canine alveolus; slightly anterior to this, the smaller foramen lies above the symphysial surface. The recent opossum, *Didelphis*, has similar nutrient foramina. In this and other recent didelphines, the symphysis is not rigidly fused and relative movement of the two rami can take place. The foramina supply small blood vessels to connective tissue around the two symphysial surfaces. A similar condition evidently existed in these fossil forms.

[1] Since this manuscript was submitted, the author's attention has been drawn to a paper by Von Koenigswald (1970). In this work, the cranial anatomy of *Peratherium* is compared with that of recent didelphids and the various species from the Upper Oligocene and Miocene of Europe are described.

Except for S.M. C30707, little of the posterior part of the mandible is preserved. In B.M. 30350 and S.M. C53476, the base of the masseteric fossa is preserved, bounded by strong condyloid and coronid crests. The mandibular foramen lies just below alveolar level. In B.M. 30350, the base of the angular process is inturned and shelf-like. S.M. C30707 comprises two fragments joined posterior to M_4. The fit is not good and both pieces may not belong to the same individual. The posterior region,

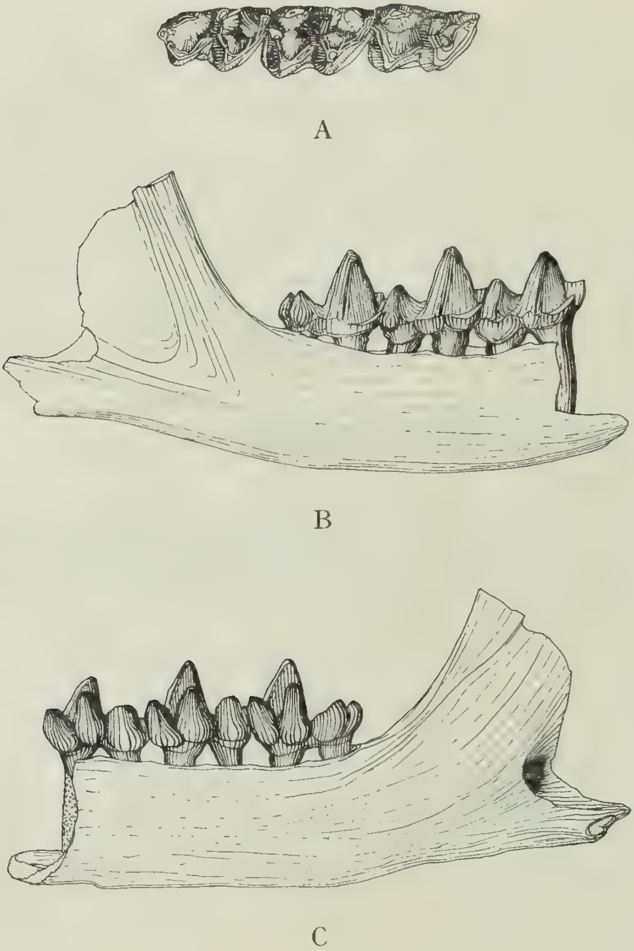

Fig. 9. '*Peratherium* species A'. Fragmentary right mandibular ramus with M_2–M_4. B.M. 30350 ×8. Lower Headon Beds, Hordle Cliff. (A) Occlusal view. (B) External view. (C) Internal view.

however, on size can be assigned to this species although there are structural differences from B.M. 30350 which may be due to variation in individual age: the coronoid process slopes more gently; the mandibular foramen is more baso-anteriorly sited and there is a larger space between the coronoid and M_4. The convex transversely-elongated condyle lies just above alveolar level (S.M. C30707) and is separated from the coronoid by a prominent notch.

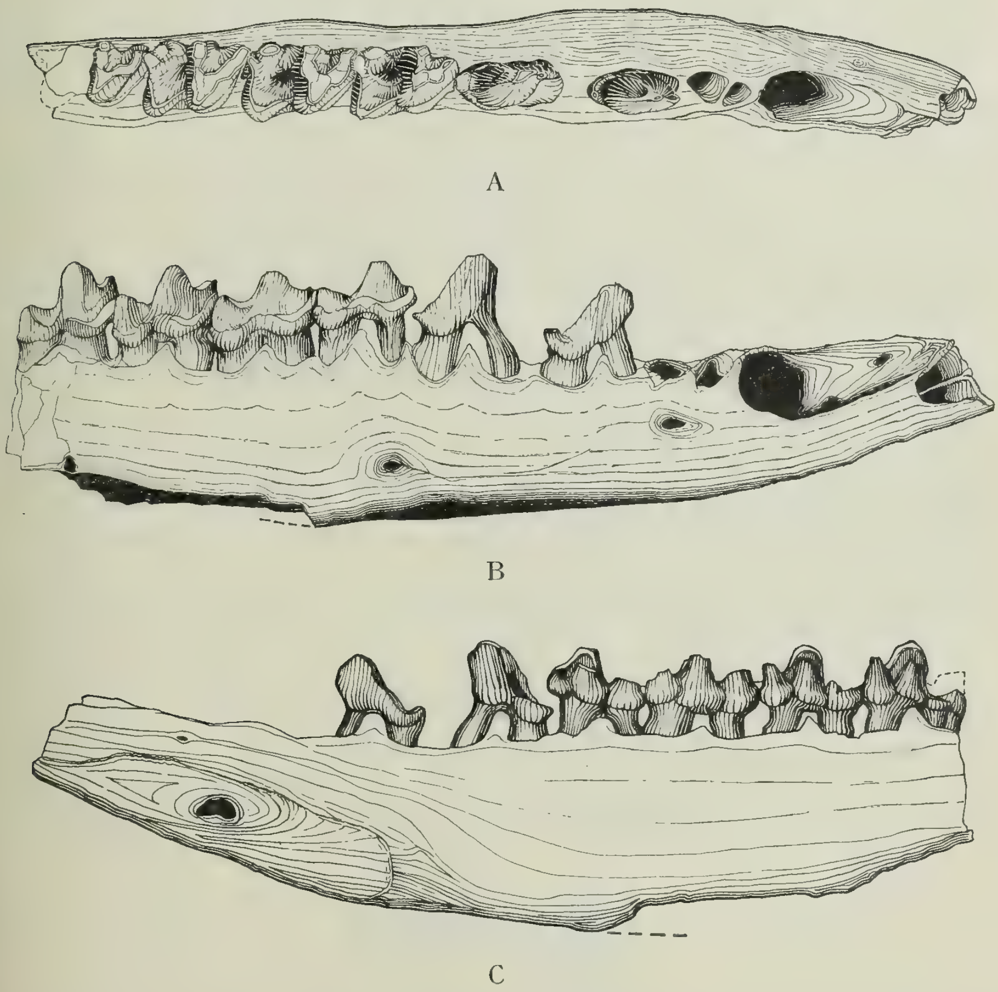

Fig. 10. '*Peratherium* species A'. Fragmentary right mandibular ramus with P_2–M_4. S.M.C30707 approx. × 8. Lower Headon Beds, Hordle Cliff. (A) Occlusal view. (B) External view. (C) Internal view.

The four molars form a continuous series internally, the hypoconulid of one molar fitting closely against the external cingulum of the adjacent posterior tooth. M_1–M_3 are subequal in size; M_4 is of similar length but with a narrower talonid. M_4 is rectangular in outline with subequal talonid and trigonid. The trigonid is only moderately elevated, the posterior wall falling steeply to the basined talonid. The protoconid is the largest cusp, the metaconid intermediate and the paraconid smallest. There is a prominent antero-external cingulum. The paraconid, which forms the sharp antero-internal extremity of the tooth, is strongly internal, lying on an antero-posterior line with the metaconid and entoconid; it is completely separated from the metaconid. The deeply-basined talonid bears a subequal hypoconid and entoconid and a smaller hypoconulid; this hypoconulid is intermediate between the median and internal positions and posterior to the hypoconid and entoconid. A small antero-posterior crest runs from the entoconid to the posterior trigonid wall from which it is separated by a small valley. Similar crests connect the hypoconulid to the hypoconid and entoconid. There is a small crista obliqua. A strong antero-external cingulum is pressed up against and external to the projecting hypoconulid of the anterior tooth; it runs below the protoconid and hypoconid, to the base of the hypoconulid. M_3 is structurally almost identical with M_4, except that the tooth is somewhat wider transversely. M_2 is structurally nearly identical with M_3. M_1 is similar but a little smaller in size.

P_3 bears a prominent single anterior cusp which is crested anteriorly. Posteriorly two crests fall from the cusp to a small internally-shifted talonid. P_2 is smaller but structurally very similar to P_3 and separated from it by a marked diastema. P_1 is separated from P_2 by a small diastema; the tooth is represented in S.M. C30707 by two alveoli, the anterior one situated rather external to the tooth row. In S.M. C30707 the canine alveolus indicates a large semi-procumbent tooth. Anterior to this, a large alveolus subdivided into three, may indicate the positions of three closely-spaced incisors.

Two isolated upper teeth considered as M^2 and M^3 are known from the Headon Beds. M^3 is distinguished from M^2 by having a sharper internal apex and by being more compressed antero-posteriorly. In M^3 the paracone is slightly smaller than the metacone, but larger than the protocone. The metacone is directly posterior to the paracone, both cusps lying slightly external to the longitudinal midline. The paracone and metacone are crested externally, giving both cusps a strong V-shaped appearance: the postero-external paracone crest and the antero-external metacone crest meet on the antero-posterior midline; the sharp antero-external paracone

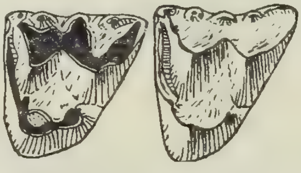

FIG. 11. '*Peratherium* species A'. Occlusal view of composite left M^2–M^3 ×10. M^2 (S.M. C54170) and M^3 (S.M. C54171). Lower Headon Beds, Hordle Cliff.

crest meets the antero-external stylar cusp and the postero-external metacone crest forms the sharp postero-external tooth margin. From the antero-internal protocone a crest runs antero-externally, dilating into a small but distinct paraconule just internal to the paracone base; the crest continues antero-externally as a cingular shelf at the base of the anterior wall of the paraconid. A similar crest runs from the protocone, swelling into a metaconule just internal to the metacone base; the metaconule is larger than the paraconule.

There are four well-developed rounded stylar cusps on the external cingular margin: stylar cusp A on the antero-external extremity of the tooth is joined to the antero-external paracone crest; the larger more elongated stylar cusp B is well separated from cusp A; stylar cusp C, subequal with cusp B, lies on the transverse midline of the tooth; stylar cusp D, smaller and less distinct than C, continues as a small crest to the postero-external extremity of the tooth. Stylar cusp E is absent. The external margin is slightly embayed in the region of stylar cusp C. The area between protocone, metacone and paracone is strongly basined, and to a lesser extent, between the metacone/paracone and the external stylar cusps.

M^2 is similar to M^3 but there are several minor differences: the tooth is slightly longer antero-posteriorly; the metacone is more markedly larger than the paracone; the paracone and metacone are subequal; the conules are stronger, the metaconule giving the tooth a more blunted appearance internally, and stylar cusp A is smaller and cusp B larger, although cusp C is still larger than cusp D.

REMARKS. The bulk of the material is from the Lower Headon Beds of Hordle Cliff. The exact horizon and locality are unknown, but a coarse white sand matrix on some specimens indicates possible derivation from the Crocodile Bed. Two specimens from the Isle of Wight extend the species range into the Upper Headon Beds. The isolated upper molars are referred to this species because of similar dimensions and good occlusion with the lower molars.

There is little variation in the teeth dimensions in this material. S.M. C53476 and S.M. C30707 have much deeper mandibles but also more wear on the teeth,

TABLE 5

Measurements (in mm) of '*Peratherium* species A'

	P_2		P_3		M_1		M_2		M_3		M_4	
	a-p	trs	a-p	trs	a-p	trs	a-p	trs	a-p	trs	a-p	trs
B.M. 30350	—	—	—	—	—	—	1·7	1·2	1·9	1·1	1·8	1·0
F.C.S. 2	—	—	—	—	—	—	—	—	1·95	1·3	—	—
B.M. M26050	—	—	—	—	—	—	—	—	2·0	1·3	—	—
S.M. C30707	1·3	0·7	1·5	0·75	1·6	1·1	1·7	1·2	1·7	1·1	—	1·0
S.M. C53476	—	—	—	—	—	—	1·6	1·35	1·8	1·3	—	—
S.M. C30708	—	—	—	—	—	—	—	—	1·85	1·05	—	—
B.M. 36812b	—	—	—	—	—	—	—	—	—	—	1·8	0·9
B.M. 30348	—	—	—	—	—	—	—	—	1·9	1·2	1·8	1·0

	M^2		M^3	
	a-p	trs	a-p	trs
S.M. C54171	—	—	1·8	2·0
S.M. C54170	1·95	2·0	—	—

which may indicate a greater individual age. Hough observed (1961), that in recent didelphids, spaces tend to appear between the premolars in the mature adult. This feature of the premolars in S.M. C30707, may be similarly a variation due to individual age.

'*Peratherium* species B'

(Text-fig. 12)

MATERIAL. All specimens, except where otherwise stated, are from the Lower Headon Beds (Mammal/Crocodile Bed), Hordle Cliff.

B.M. 13250 (2). Fragment of left mandibular ramus with M_2–M_4 and the basal part of the coronoid. Teeth badly worn.

B.M. M13251. Fragment of left mandibular ramus with M_2–M_4 and alveoli of C–P_3 and M_1. Teeth badly worn.

B.M. 13250 (3). Fragment of right mandibular ramus with M_3–M_4. Teeth badly worn.

S.M. C54155. Fragment of left mandibular ramus with M_1–M_2 and alveoli of M_3. Teeth badly worn. Lower Headon Beds, Hordle Cliff. The Sedgwick Museum label gives 'Rodent Bed' as the locality but the preservation and adhering white sand suggests probable derivation from the Mammal/Crocodile Bed.

S.M. C53474. Anterior fragment of left mandibular ramus with M_2 and alveoli of the canine (base), P_1–M_1 and M_3. Teeth moderately worn.

B.M. 44142 (1). Fragment of right mandibular ramus lacking teeth, with alveoli of P_1–M_4.

(2). Small fragment of right mandibular ramus with alveoli of uncertain position in the tooth row.

S.M. C53480. Fragment of right mandibular ramus with posterior root of M_2 and the roots of M_3–M_4.

S.M. C54169. Isolated trigonid fragment of left lower molar. Badly worn. Lower Headon Beds (Rodent Bed), Hordle Cliff.

DESCRIPTION. The posterior mental foramen lies below M_1 (B.M. M13251) or M_2 (S.M. C53474); the anterior mental foramen is situated below P_1 (B.M. M13251) or P_2 (S.M. C53474). The subhorizontal symphysial surface extends to below P_2. S.M. C53474 possesses a nutrient foramen (as in S.M. C30707, referred to '*Peratherium* species A') opening through the symphysial surface.

No description is given of the dentition which is structurally almost identical to previously described specimens referred to '*Peratherium* species A'.

REMARKS. Because of the much larger dimensions of the teeth (especially the length of the tooth row) compared with '*Peratherium* species A', these specimens are considered to represent a distinct species. Hough stated (1961), that this criterion is less subject to variation than depth of mandible and spacing of premolars, and has been used in the determination of *Marmosa* species. There is some variation in mandible depth and premolar spacing; as in '*Peratherium* species A' this probably reflects individual age differences.

Two mandibular fragments without teeth (B.M. 44142 (2) and S.M. C53480) are tentatively referred to this species. B.M. 44142 (1) is considerably longer and more slender than the other referred specimens with widely spaced anterior premolars; it is considered tentatively as an old adult of '*Peratherium* species B'.

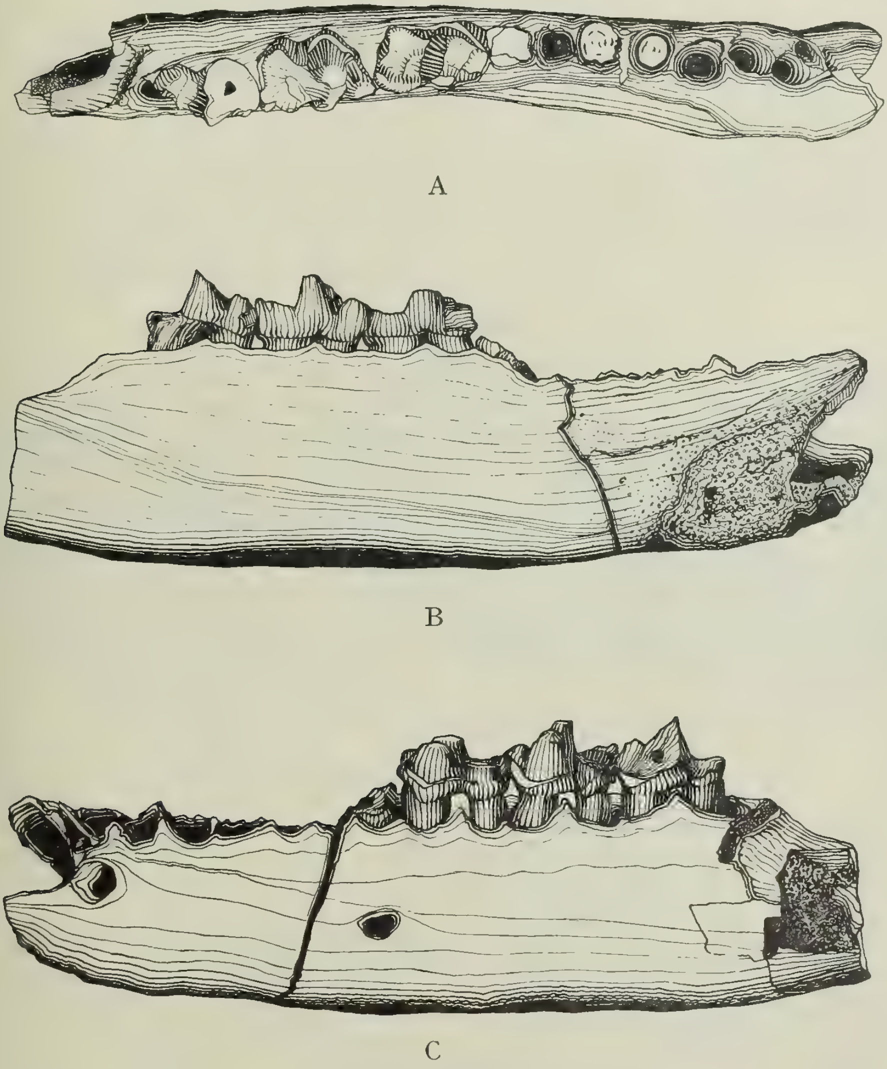

Fig. 12. '*Peratherium* species B'. Fragmentary left mandibular ramus with M_2–M_4. B.M. M13251 ×6. Lower Headon Beds, Hordle Cliff. (A) Occlusal view. (B) Internal view. (C) External view.

A pathological condition is seen in S.M. C53480. The mandible evidently had been damaged during life internally below M_2 and M_3, and shows some formation of callus in this area.

TABLE 6

Measurements (in mm) of '*Peratherium* species B'

	M_1		M_2		M_3		M_4	
	a-p	trs	a-p	trs	a-p	trs	a-p	trs
B.M. 13250 (2)	—	—	2·5	1·75	2·5	1·6	2·5	1·4
B.M. M13251	—	—	2·5	1·6	2·55	1·6	2·25	1·4
B.M. 13250 (3)	—	—	—	—	2·5	1·5	2·5	1·35
S.M. C53474	—	—	2·6	1·4	—	—	—	—
S.M. C54155	2·7	1·4	2·7	1·7	—	—	—	—

Order INSECTIVORA

Family **NYCTITHERIIDAE** Simpson, 1928

REMARKS. Simpson's family Nyctitheriidae was abandoned by McKenna (1960a) as an unnatural unit. Van Valen (1967) placed *Nyctitherium* together with *Clinopternodus* Clark, 1937, as a subfamily (Nyctitheriinae) within the Adapisoricidae. On the basis of Robinson's (then unpublished) work on the group, McKenna (1968) recognised 'a restricted family-group taxon based on *Nyctitherium* and several referred genera', into which he placed *Leptacodon*. In his review of the family, Robinson (1968) upheld the status of Simpson's family Nyctitheriidae, subdividing it into three subfamilies: Nyctitheriinae Simpson, 1928; Geolabidinae McKenna, 1960; and Micropternodontinae (Stirton & Rensberger, 1964). The Geolabidinae, placed originally by McKenna (1960b) in the Erinaceidae, had been grouped by Van Valen (1967) within the Adapisoricidae. Robinson's view is adopted here.

Subfamily **NYCTITHERIINAE** Simpson, 1928

DIAGNOSIS. P^4_4 semi-molariform, P_2, P_3 with two roots each, P_1 with one root, jaw long and slender, with no apparent shortening. Probable dental formula $\frac{?}{3}, \frac{?}{1}, \frac{4}{4}, \frac{3}{3}.$ (Robinson, 1968 : 129).

REMARKS. Three genera were included by Robinson (1968) in the subfamily:

Nyctitherium Marsh, 1872. Middle—Late Eocene; North America.

Leptacodon Matthew & Granger, 1921. Middle (?), Late Palaeocene—Early Eocene; North America.

Saturninia Stehlin, 1940. Late Eocene; Europe.

To these are added two new genera described below.

Leptacodon has undergone a varied history. McKenna (1960a : 52 and 1960b : 156) removed *Leptacodon* (*sensu stricto*) from the Leptictidae; this genus, composed of *L.*

tener Matthew & Granger, 1921 (the type species); *L. ladae* Simpson, 1935 (apparently, but not mentioned specifically by McKenna); *L. minutus* Jepsen, 1930, and *L. jepseni* McKenna, 1960a, was considered to be near the base of erinaceid phylogeny and possibly closely related to the ancestry of the Geolabidinae. This tentative reference of *Leptacodon* (*sensu stricto*) to the Geolabidinae was accepted by Russell (1964 : 46). Van Valen (1967) placed *Leptacodon* (*sensu stricto*) in the Adapisoricidae (subfamily Adapisoricinae) and more recently, McKenna (1968) has stated that the genus is perhaps best considered as a nyctithere. Robinson (1968) in his review of the Nyctitheriidae, clarified the systematics of the genus *Nyctitherium;* he indicated that the type specimen of *Myolestes dasypelix* Matthew, 1909, is a nyctitherine, although he has agreed with McKenna's allocation of a referred specimen 'c.f. *Myolestes dasypelix*' to the Geolabidinae (McKenna, 1960b : 147). In addition to *Nyctitherium dasypelix*, Robinson (1968) recognised two further species: the type species, *N. velox* Marsh, 1872, and *N. serotinum* (Marsh, 1872). In the same paper, he rejected Stehlin's reference of *Saturninia* to the Soricidae, maintaining for the genus, a close relationship with *Nyctitherium.*

Genus ***SCRAEVA*** gen. nov.

ETYMOLOGY. Screawa—(Anglo-Saxon), a shrew.

DIAGNOSIS. In P_4–M_3, talonid narrower transversely than trigonid; talonid and trigonid subequal in length; trigonid with markedly angular outline, with straight or slightly convex internal margin and moderately to sharply pointed anterior apex; protoconid larger than metaconid; talonid angular with internal and external margins subparallel, except on M_3. M_1–M_3 with a mesoconid; hypoconid and entoconid subequal in size; hypoconulid median or slightly internal of midline, in M_3 posteriorly projecting as a prominent rounded lobe. P_4 hypoconulid minute, slightly external to midline. Internal face of coronoid process with antero-posterior ridge at molar alveoli level.

TYPE SPECIES. *Scraeva hatherwoodensis* sp. nov. Upper Headon Beds (*Microchoerus* Bed), Headon Hill.

REMARKS. One other species has been distinguished: *Scraeva woodi* sp. nov. Lower Headon Beds (Mammal/Crocodile Bed), Hordle Cliff.

In 1844, Charlesworth (*in* Wood, 1844 : 350, footnote) recorded a fragmentary mandibular ramus, obtained by Flower from Hordle Cliff, which he named *Spalacodon;* this was again recorded by Charlesworth (1845 : 50). A year later, the specimen was figured by Wood (1846, pl. 2, figs 5, 5a-c) and listed as 'an imperfect lower jaw'. Charlesworth and Wood did not designate a species and the specimen was referred to as '*Spalacodon*' or '*Spalacodon* sp.' Because of the inadequate original descriptions and the loss of the specimen, *Spalacodon* is considered here to be a *nomen nudum.* Comparison of the type material of *Scraeva woodi* with Wood's illustrations indicate the probable specific identity of the two forms. This contention is strengthened by the probability that *Spalacodon* and the material of *Scraeva woodi* were obtained from the same level, the Crocodile Bed of Hordle Cliff. The specimen described by

Charlesworth and Wood (from Wood's figures, a right mandibular ramus with P_2 and P_4–M_3) has not been located during the present study and the material is considered to be lost.

Scraeva is referred to the Nyctitheriidae mainly on the basis of strong resemblances to *Leptacodon* and *Nyctitherium.* The soricid-like antero-posterior internal ridge on the coronoid, characteristic of *Nyctitherium* (Robinson, 1968), is well developed in *Scraeva.* A talpid characteristic, occasionally developed in *Nyctitherium* and present also in *Saturninia*, is a continuation of the crista obliqua up the posterior wall of the metaconid; this is prominently and invariably developed in *Scraeva.* The Headon genus is distinguished from other nyctitheres as follows: In *Nyctitherium* (see Robinson, 1968), P_4 has a smaller talonid basin and lacks an entoconid; in the molars, the hypoconulid is more internal in position and smaller and the paraconid is more internally situated. In this study the type specimen of *Saturninia* has not been examined, but from Stehlin's illustrations (1940, fig. 1c, fig. 2c) the P_4 is relatively smaller with a less basined talonid, and the molar paraconids are more internal in position. In addition, in both *Nyctitherium* and *Saturninia*, the outline of P_4–M_3 is more rounded and the P_4–M_3 trigonid and talonid are of similar transverse width.

The P_4 of *Scraeva* is very similar to that of the type species of *Leptacodon*, *L. tener*, except for a rounded posterior talonid margin and a sharper, more separated paraconid in *Leptacodon tener.* The molars are also similar although in *Leptacodon tener*, the metaconid is as high as the protoconid; the paraconid is somewhat sharper and more separated; the M_3 hypoconulid is less projecting posteriorly and the trigonid cusps are not so elevated above the talonid. Less resemblance is apparent in the P_4 of *Leptacodon ladae* which has a more isolated median paraconid, a more anteriorly placed protoconid and a much shorter talonid.

Scraeva also shows marked resemblances to *Scenopagus* McKenna & Simpson, 1959, *Messelina* Tobien, 1962, and *Adapisorex* Lemoine, 1883; these genera have been generally regarded as 'primitive probable erinaceids', although extensive regrouping and familial separation from the Erinaceidae has been proposed by Van Valen (1967 : 261). In several respects, particularly the elevated trigonids and the structure of M_3, *Scraeva* is similar to *Scenopagus* but there are significant differences: in *Scenopagus*, the talonid cusps of the molars are slightly higher; the trigonid cusps are compressed antero-posteriorly and the paraconid crest is larger and more oblique, resulting in a blunter anterior tooth apex; the hypoconid crest runs to the internal base of the protoconid, not the metaconid as in *Scraeva*, and the hypoconulid is only slightly developed in M_1–M_2. P_4 has not been adequately described or figured. In *Messelina*, the lower molars are much narrower transversely; the talonid and trigonid are subequal in width and the hypoconulid is internal; the trigonid of the molars is not elevated, and in M_1–M_2 the trigonid and talonid cusps are subequal in height. Also, the P_4 of *Messelina* has a rounded outline and lacks a hypoconulid. Greater resemblance to *Scraeva* is seen in *Adapisorex:* in the molars of both genera, the protoconid is larger than the metaconid (but not so extremely developed in *Scraeva*) and the basined talonid has a median hypoconulid. The P_4 is similar in *Scraeva* and *Adapisorex*, with a small metaconid, a large protoconid anterior to the metaconid which dominates the trigonid (less extremely so in *Scraeva*) and a small median hypoconulid. However, *Adapisorex* is distinguished from *Scraeva* by having much lower-placed cusps, the trigonid being little elevated above the talonid; the entoconid and hypoconid are much larger and the trigonid and talonid are subequal in width.

In basic structure, particularly of P_4–M_2, *Adunator* Russell, 1964 (originally considered by Russell as a leptictid but placed by Van Valen, 1967, in the Adapisoricinae) shows similarities to *Scraeva*, although the P_4 paraconid is much more separated anteriorly as a distinct cusp. Also, in *Adunator* the M_3 hypoconulid is more internal and not so projecting as an isolated lobe, and in the molars the metaconid and entoconid are higher than the protoconid and hypoconid respectively.

Scraeva hatherwoodensis sp. nov.

(Text-fig. 13)

ETYMOLOGY. hatherwoodensis—from Hatherwood Point, off Headon Hill, Isle of Wight, the sea cliff locality.

DIAGNOSIS. The smaller species. P_4–M_2 trigonid with a slight posterior tilt. P_4–M_2 with straight internal trigonid margin and protoconid and metaconid more internally placed than in *S. woodi*. P_4 metaconid and protoconid slightly lower than corresponding cusps of M_1; paraconid median, at same height as molar paraconids. P_4 metaconid more posteriorly placed in relation to protoconid than in *S. woodi*, in M_1 metaconid only slightly posterior to protoconid.

HOLOTYPE. B.M. M26051. Fragment of left mandibular ramus with P_4–M_2 and alveoli of I_3–P_3 and M_3. Lower external surface embedded in matrix. Teeth slightly worn. Upper Headon Beds (*Microchoerus* Bed), Headon Hill. The only specimen of the species.

DESCRIPTION. The long slender mandible has a large oval posterior mental foramen just below the alveolar level of P_3. There is a small angular process (tip damaged on the specimen) at molar alveoli level. The coronoid and condyle are not preserved. The mandibular foramen is visible just below alveolar level. On the internal face of the coronoid, a prominent antero-posterior ridge runs from the level of the M_3 alveoli towards the mandibular foramen. A similar ridge was observed by Simpson (*in* McGrew, 1959) on a toothless mandibular fragment from the Middle Eocene of Wyoming, tentatively referred to the Soricidae. This structure also occurs in *Nyctitherium* (Robinson, 1968 : 130).

M_3 is double-rooted and known only by alveoli. In M_1–M_2 the talonid and trigonid are subequal in length, but the talonid is narrower transversely. The internal and external talonid margins are straight and subparallel. The trigonid is angular with a sharp anterior apex and a straight internal margin; sharply elevated, it falls almost vertically to a low basined talonid. There is a prominent antero-external cingulum.

The protoconid is larger than the metaconid and slightly more anteriorly placed (on both M_1 and M_2 the metaconid is damaged). The paraconid is moderately well separated and cuspate, forming the sharp anterior extremity of the trigonid; this cusp is median in M_1 but slightly internal to this position in M_2. The hypoconid and entoconid are subequal; the hypoconulid is a little smaller but comparison is difficult as the entoconid is almost unworn, whereas the hypoconid and hypoconulid are badly worn. The median hypoconulid (in M_2 slightly internal to the midline) is posterior to the hypoconid and entoconid, projecting very slightly posteriorly and joined to the hypoconid and entoconid by small low crests. From the entoconid a low feeble crest runs anteriorly to the metaconid base. A stronger crista obliqua runs from the hypoconid up the posterior wall of the metaconid; this crest swells into a prominent mesoconid (stronger on M_1 than M_2) midway along its length.

P_4 is very similar to M_1 and M_2 but differs in several respects: the tooth is more laterally compressed and smaller in all dimensions; the hypoconulid is very small, situated external to the midline near the hypoconid; the metaconid is more posterior in relation to the protoconid; the hypoconid is larger than the entoconid and the protoconid/paraconid crest is smaller, placed slightly external to the midline and less V-shaped than in the molars. P_3 and P_2 are represented only by alveoli; these teeth were apparently double-rooted and closely spaced. P_1 is single-rooted, represented only by the alveolus. Known only from the alveolus, the canine was evidently slightly anteriorly inclined, with a root diameter as that of P_1. I_3 is represented by the possible base of the alveolus.

REMARKS. This species is clearly related to *Scraeva woodi* in that both forms exhibit the characteristic squared angular outlines of the teeth. There are a number of small but distinct differences between *S. hatherwoodensis* and *S. woodi* (see diagnoses) which indicate at least a specific separation. Also, *S. woodi* is markedly larger.

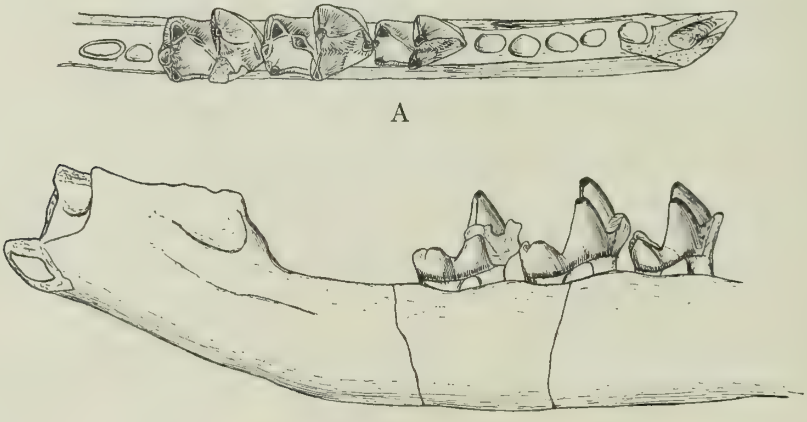

FIG. 13. *Scraeva hatherwoodensis* gen. et sp. nov. Fragmentary left mandibular ramus with P_4–M_2. Holotype (B.M. M26051) × 10. Upper Headon Beds, Headon Hill. (A) Occlusal view. (B) Internal view.

TABLE 7

Measurements (in mm) of *Scraeva hatherwoodensis*

	P_4		M_1		M_2	
	a-p	trs	a-p	trs	a-p	trs
Holotype (B.M. M26051)	1·35	0·9	1·5	1·1	1·5	1·2

Scraeva woodi sp. nov.

(Text-fig. 14)

ETYMOLOGY. woodi—after Searles Wood who first listed and figured insectivore material from the Headon Beds as *Spalacodon,* a name suggested by Charlesworth, but here considered as a *nomen nudem.*

DIAGNOSIS. Larger than *S. hatherwoodensis.* P_4 with slightly concave internal trigonid margin, in molars slightly convex. P_4 metaconid and protoconid same height as corresponding cusps of M_1; paraconid markedly internal, lower than molar paraconids. P_4 metaconid slightly posteriorly placed in relation to protoconid, in M_1 metaconid opposite and in M_2–M_3 metaconid slightly anterior to protoconid.

HOLOTYPE. S.M. C53475. Fragment of left mandibular ramus with P_4–M_3 and alveoli of P_3. Teeth unworn. Lower Headon Beds (Mammal/Crocodile Bed), Hordle Cliff.

PARATYPE. B.M. M25112. Left mandibular ramus with P_2, P_4–M_3 and alveoli of I_2–P_1, P_3. Badly worn dentition. Lower Headon Beds (Mammal/Crocodile Bed), Hordle Cliff.

MATERIAL. S.M. C30709. Fragment of left mandibular ramus with M_1–M_2, posterior alveolus of P_4, and alveoli of M_3. Teeth unworn but metaconids damaged. Lower Headon Beds (Mammal/Crocodile Bed), Hordle Cliff.

B.M. 36801c. Fragment of left mandibular ramus with M_2 and alveoli of M_3 Internal margin of tooth damaged and tips of cusps broken off. Patches of coarse white sand matrix adhering. Lower Headon Beds (Mammal/Crocodile Bed), Hordle Cliff.

S.M. C54168. Isolated right M_2. Slightly worn. Lower Headon Beds (Rodent Bed), Hordle Cliff.

DESCRIPTION. The mandible is a little stouter than in *S. hatherwoodensis,* with a large oval posterior mental foramen below the posterior root of P_3. The antero-posterior ridge on the internal face of the coronoid is present as in *S. hatherwoodensis.* Paratype B.M. M25112 shows the wedge-shaped symphysial surface with ridged margins; this occupies nearly the whole depth of the jaw under I_2, sloping baso-posteriorly to below the anterior root of P_2.

The incisors, canine and P_1 are known only from alveoli in paratype B.M. M25112. In this specimen, two distinct, well-separated alveoli both slightly smaller than the P_1 alveolus, indicate at least two incisors, here considered as I_2–I_3. Another more anterior tooth may have been present but evidence is lacking. The canine is represented by an alveolus indicating a larger anteriorly-inclined tooth. P_1, single-rooted and well-separated, is represented by the alveolus which is smaller than that of the canine. P_2 is double-rooted and oval in outline. A single large anterior median cusp slopes antero-basally to a small low antero-internal cuspule; a small heel bears a minute internal cuspule. P_3 is known only from the alveoli; the tooth is double-rooted and apparently about the same size as P_2.

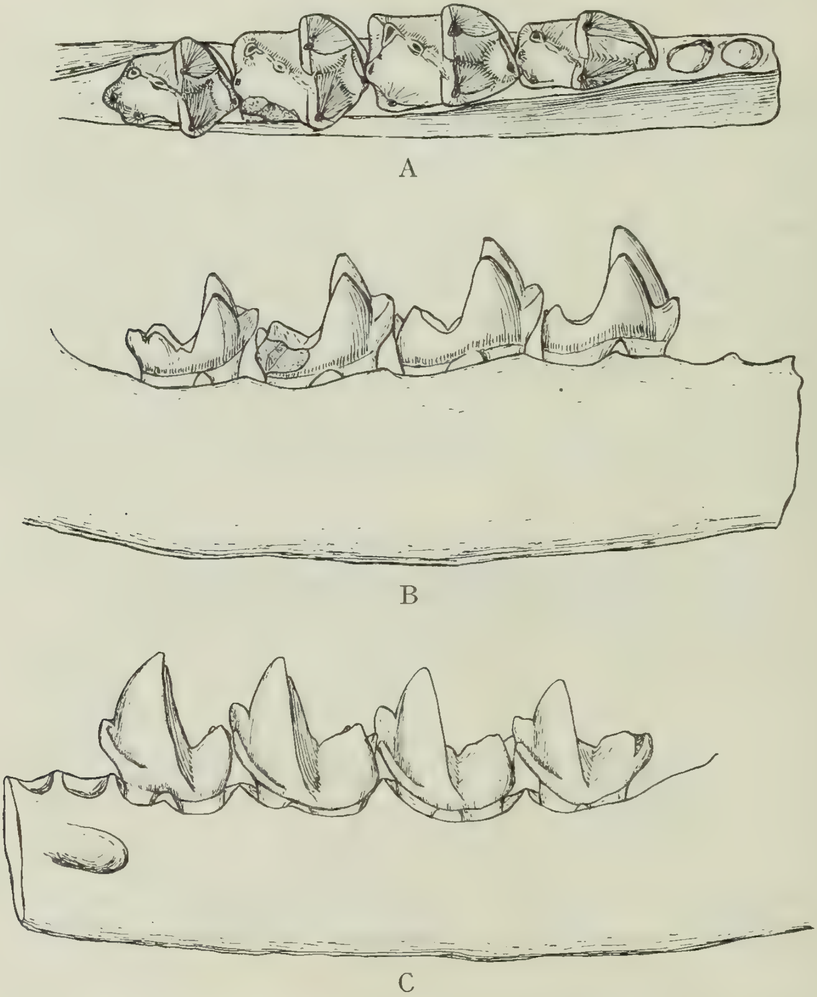

FIG. 14. *Scraeva woodi* gen. et sp. nov. Fragmentary left mandibular ramus with P_4–M_3. Holotype (S.M. C53475) × 10. Lower Headon Beds, Hordle Cliff. (A) Occlusal view. (B) Internal view. (C) External view.

The trigonid and talonid in P_4 are subequal in length. In M_1–M_3 the talonid is slightly more elongated antero-posteriorly and narrower transversely; the internal and external margins are fairly straight and subparallel, except in M_3 where the talonid narrows posteriorly (not as extreme as in *S hatherwoodensis*). The M_2 in paratype B.M. M25112 has a somewhat indented external margin. P_4 and M_3 are narrower transversely than M_1 and M_2. In P_4–M_3 the trigonid is angular with only a slightly curved internal margin; sharply elevated, it drops steeply to a low basined talonid. There is a prominent antero-external cingulum as in *S. hatherwoodensis*. The metaconid is smaller than the protoconid, situated posterior to the protoconid in P_4, opposite in M_1 and slightly anterior in M_2 and M_3. The paraconid, moderately well separated and cuspate, forms the fairly sharp antero-internal extremity of the tooth—this cusp is moderately internal to the midline in all teeth (P_4–M_3). The hypoconulid in M_1 and M_2 is a little smaller than the entoconid and median in position; in P_4, it is very small and slightly external to the midline (but in M_3, hypoconulid, entoconid and hypoconid are subequal). The P_4 hypoconulid in paratype B.M. M25112 is indistinct, indicated only by a slight externally situated projection posterior to the hypoconid and entoconid. M_3 has a posteriorly projecting hypoconulid lobe, slightly internal to the midline; this lobe is very prominent and apically projecting in paratype B.M. M25112. In P_4–M_3 the hypoconulid is joined to the hypoconid and entoconid by small low crests; a low feeble crest runs antero-internally from the entoconid to the metaconid base. A much stronger crista obliqua runs from the hypoconid up the posterior wall of the metaconid; this crest bears a distinct mesoconid in M_1–M_3, although the cusp is only feebly developed in M_2.

REMARKS. Comparison with *S. hatherwoodensis* has been effected in the diagnosis and description. Only five specimens are known and little idea can be gained of variation within the species. S.M. C30709 and S.M. C54168 differ from the holotype only by having a less distinct mesoconid in the molars. Paratype B.M. M25112 represents a much older individual than the holotype and comparison of the two specimens is difficult because of a high degree of wear on the former specimen. Reference of B.M. M25112 to the species is fairly certain, however; when structural differences which can be assigned to excessive wear are discounted, the two specimens have a high degree of similarity. Also, both specimens are apparently from the same locality and approximate horizon. B.M. 36801c appears closely similar to the holotype, although the former specimen is damaged.

TABLE 8

Measurements (in mm) of *Scraeva woodi*

	P_2		P_3		P_4		M_1		M_2		M_3	
	a-p	trs	a-p	trs	a-p	trs	a-p	trs	a-p	trs	a-p	trs
B.M. M25112	1·45	0·6	—	—	1·7	1·05	1·75	1·45	1·8	1·45	1·8	1·2
B.M. 36801c	—	—	—	—	—	—	—	—	1·7	1·15	—	—
S.M. C54168	—	—	—	—	—	—	—	—	1·8	1·25	—	—
S.M. C53475	—	—	—	—	1·6	1·0	1·95	1·3	1·85	1·4	1·8	1·2
S.M. C30709	—	—	—	—	—	—	1·8	1·15	1·7	1·25	—	—

Genus ***ARVALDUS*** gen. nov.

Etymology. Arvaldus—Jutian king of the Isle of Wight, A.D. 686.

Diagnosis. P_4 protoconid markedly anterior to the metaconid; hypoconulid (damaged) appears more prominent than in *Scraeva*. P_4–M_3 posterior margin somewhat oblique to length of tooth row; paraconid internal; protoconid larger than metaconid; P_4 hypoconid opposite, M_1–M_2 slightly posterior, and in M_3 markedly posterior to entoconid. M_3 hypoconulid prominent, internal to midline, slightly projecting; talonid angular in outline with straight posterior and postero-internal margins.

Type species. *Arvaldus stintoni* sp. nov. Upper Headon Beds (Lignite Bed), Headon Hill. The only known species.

Remarks. *Arvaldus* shows considerable similarity with *Leptacodon*, *Nyctitherium* and *Saturninia*. The P_4 of *Leptacodon tener* (the type species) seems quite close to that of *Arvaldus* with a well differentiated talonid and the protoconid strongly anterior to the metaconid, although in P_4 of *L. tener*, a hypoconulid is absent and the posterior talonid margin has a rounded outline. Similarity with the P_4 of *Leptacodon ladae* is shown by the anterior position of the protoconid and the presence of a small hypoconulid, although in several other respects—the median paraconid, rounded outline and small talonid, the tooth is rather different. The type species of *Nyctitherium*, *N. velox*, is distinguished from *Arvaldus* by the P_4 talonid being much shorter antero-posteriorly with the protoconid opposite the metaconid; in the molars, the paraconid is more internal and the hypoconulid is weaker and placed more internally, although in this latter respect, *Arvaldus* is closer to *N. serotinum* where the molar hypoconulid is slightly more median in position. In *Saturninia* the P_4 protoconid is opposite the metaconid and the paraconid of the molars is more internally situated.

One of the most obvious features which distinguishes *Leptacodon*, *Nyctitherium*, *Saturninia* and *Scraeva* from *Arvaldus* is the structure of M_3. In *Leptacodon* there is a strong entoconid opposite the hypoconid and a well separated posteriorly projecting hypoconulid. This tooth in *Nyctitherium velox* is different in outline; the talonid is shorter with a median hypoconulid and an entoconid which is opposite the hypoconid. The M_3 talonid in *Saturninia* is shorter and different in outline with a median posteriorly projecting hypoconulid. In M_3 of *Scraeva* the entoconid and hypoconid are opposite and there is a median posteriorly projecting hypoconulid.

In this M_3 talonid structure, *Arvaldus* shows similarities with the American geolabidines, *Geolabis*, 'c.f. *Myolestes dasypelix*' and *Centetodon*, particularly the latter. In *Centetodon*, the M_3 talonid bears only a hypoconid and an internal crestiiform hypoconulid (fused entoconid and hypoconulid?); the internal wall of the postero-internally projecting hypoconulid curves abruptly baso-posteriorly and there is no sign of an entoconid. A somewhat similar distinctive M_3 talonid structure is seen in *Arvaldus*, although here it is not so pronounced; the hypoconulid is less posteriorly situated and a small anteriorly placed entoconid is still present. However, in *Centetodon* and other geolabidines, the structure of P_4 is different: in the American forms, the P_4 protoconid and metaconid are opposite and the talonid is much reduced, with a single large internal cusp. Greater similarity to *Arvaldus* is seen in the P_4 of 'c.f. *Hypacodon* sp.' (= *Centetodon* sp.) described by McKenna (1960b : 150). Here the elongation of the tooth is similar to that in *Arvaldus* and the protoconid is anterior to the metaconid; the talonid is more developed and there is a central hypoconid and a small though distinct entoconid. Robinson (1968 : 134) has considered this specimen as an adapisoricid.

Arvaldus differs from *Scraeva* in a number of important aspects (see diagnoses), the more obvious of these being the non-angular tooth outlines, the structure of P_4 and the distinctive M_3 talonid; the two genera do not appear to be closely related. To some extent, the structure of *Arvaldus* is intermediate between nyctitherines and geolabidines and on the basis of the M_3 structure, the genus could be regarded as a primitive relatively unspecialised geolabidine. However, the molarised P_4 and the continuation of the crista obliqua up the posterior wall of the metaconid support reference to the Nyctitheriinae. The anterior lower dentition and the upper teeth of *Arvaldus* are unknown. At present the European record of the family comprises *Saturninia*, *Scraeva* and *Arvaldus*, all from the Upper Eocene. It is likely that the phyletic position of *Arvaldus* will be clarified with the discovery of nyctitheriids from the Lower Eocene of Europe.

Arvaldus stintoni gen. et sp. nov.

(Text-fig. 15)

ETYMOLOGY. stintoni—after Mr F. C. Stinton, the finder of the specimen.

DIAGNOSIS. No other species are known and the diagnosis is the same as that for the genus.

HOLOTYPE. F.C.S.I. Fragment of right mandibular ramus with P_2, P_4–M_3 and the alveoli of P_3. Upper Headon Beds (Lignite Bed), Headon Hill. The only known specimen of the species.

DESCRIPTION. The mandible has a large posterior mental foramen below P_3. The posterior region is not preserved. P_2 is very similar to that of the paratype of *Scraeva woodi* (B.M. M25112). The tooth is double-rooted and oval in outline with a large median anterior cusp, which slopes baso-anteriorly to a small low antero-external cuspule. A small low heel bears a single minute internal cuspule. Represented by only alveoli, P_3 is double-rooted and apparently a little smaller than P_2.

In P_4–M_3, the talonid is a little longer antero-posteriorly than the trigonid especially in M_3 and about the same width, with an indented internal and external margin. The trigonid has a curved internal margin. The posterior wall drops less steeply than in *Scraeva*. There is a prominent antero-external cingulum. The protoconid is larger than the metaconid and situated opposite to it in M_1–M_3; in P_4 the protoconid is markedly anterior to the metaconid. The cuspate paraconid is moderately well separated and situated internally in all four teeth as in *Scraeva woodi*. The P_4 paraconid is sharper and more anteriorly projecting than in this latter species. In P_4–M_3 the hypoconid is stouter than the entoconid; the hypoconulid is a little smaller than the entoconid or subequal, except on M_3 where it is a little larger; this cusp is slightly external to the midline in P_4, median in M_1 and slightly internal in M_2 and M_3; it is posterior to the entoconid and hypoconid and projecting slightly in all four teeth. The hypoconulid is well separated from the entoconid but is joined to the hypoconid by a small low external crest. In P_4, the hypoconid is opposite to the entoconid, in M_1 and M_2 slightly posterior and in M_3 markedly posterior. From the entoconid, a feeble crest runs antero-internally to the base of the metaconid. A stronger crista oblique runs antero-internally from the hypoconid up the posterior wall of the metaconid; this swells up midway along its length into a prominent mesoconid. The enclosed talonid is deeply basined. The posterior margin of the talonid is slightly obliqua to the length of the tooth in P_4–M_2 (a tendency also seen in paratype B.M. M25112 of *Scraeva woodi*). In M_3 the straight posterior margin runs from the sharp postero-external extremity of the talonid to the slightly more posteriorly situated hypoconulid. From this latter cusp, the straight talonid margin runs obliquely forwards to the relatively anteriorly-placed entoconid.

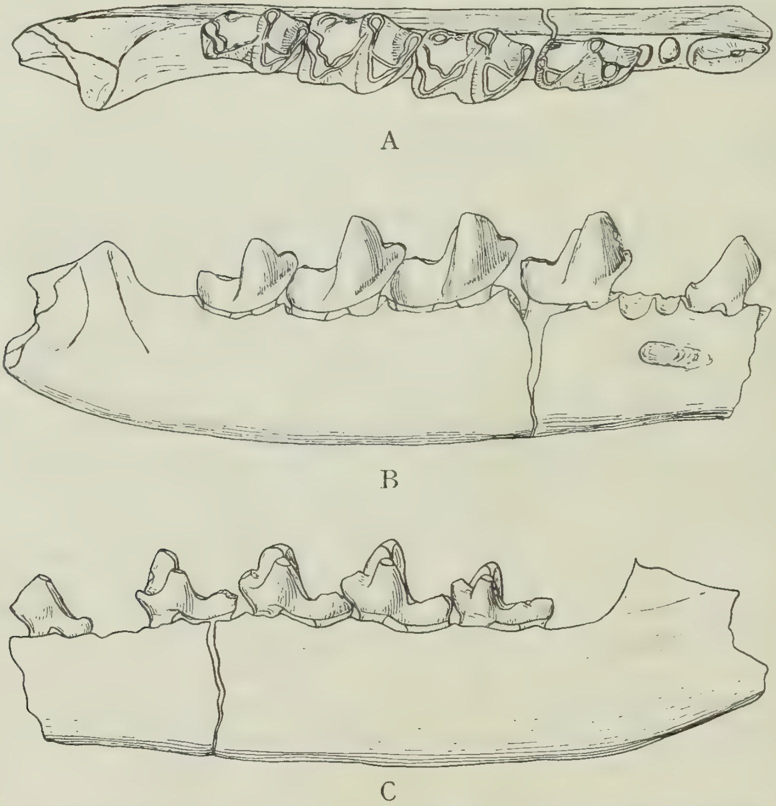

FIG. 15. *Arvaldus stintoni* gen. et sp. nov. Fragmentary right mandibular ramus with P_2, P_4–M_3. Holotype (F.C.S. 1) ×10. Upper Headon Beds, Headon Hill. (A) Occlusal view. (B) External view. (C) Internal view.

TABLE 9

Measurements (in mm) of *Arvaldus stintoni*

	P_2		P_3		P_4		M_1		M_2		M_3	
	a-p	trs	a-p	trs	a-p	trs	a-p	trs	a-p	trs	a-p	trs
Holotype (F.C.S. 1)	1·2	0·5	—	—	1·5	0·8	1·6	1·1	1·65	1·2	1·5	0·9

Family **PANTOLESTIDAE** Cope, 1884

DIAGNOSIS. Facial part of skull short, basicranial region broad, middle portion of skull elongate. Angle of mandible a short stout process expanded at the tip. Mental foramen usually beneath M_1, sometimes below P_4. Dental formula $\frac{3}{?}, \frac{1}{1}, \frac{4}{4}, \frac{3}{3}$. Molars and premolars with low massive cusps. Canines large, massive, lower canines often semiprocumbent. Upper incisors spaced and peg-like. P_1–P_3 elongate and fairly small. P_4 relatively enlarged (after Matthew, 1909).

REMARKS. On the basis mainly of differences in the structure of P_4^4, two subfamilies have been traditionally distinguished:

Pantolestinae Simpson, 1937
Pentacodontinae Simpson, 1937

Gazin (1959) erected a new subfamily, Apheliscinae; this was referred by McKenna (1960a) to the condylarths (Hyopsodontidae). Van Valen (1966) supported Gazin's reference of the Aphelescinae to the Pantolestidae, but more recently (1967) has agreed with McKenna's removal of the group to the Hyopsodontidae.

Van Valen (1967) in his revision of insectivore classification raised the pentacodonts to family level. As the justification for such a procedure (Van Valen, 1967 : 321) seems no greater than that for retaining them in the Pantolestidae, the old-established two fold subdivision of the Pantolestidae is retained here.

Subfamily **PANTOLESTINAE** Simpson, 1937

DIAGNOSIS. P_4^4 relatively little enlarged. P_4 compressed, no metaconid, semi-shearing, heel essentially unicuspid and little or not basined. P^4 with compressed amphicone, no metacone, low, sharp styles, small protocone without cingula (Simpson, 1937).

REMARKS. The Pentacodontinae are distinguishable from this subfamily by P_4^4 being much enlarged; P_4 has a well developed metaconid and basined talonid; P^4 has a distinct metacone, large protocone, with expanded cingula and styles are small or absent.

The following genera have been referred, to date, to the Pantolestinae:

Propalaeosinopa Simpson, 1927. Middle-Late Palaeocene; North America.
Bessoecetor Simpson, 1936. Middle-Late Palaeocene; North America. ?Late Palaeocene; Europe.
Pagonomus Russell, 1964. Middle-Late Palaeocene, ?Early Eocene; Europe.
Pantomimus Van Valen, 1967. Middle Palaeocene; North America.
Palaeosinopa Matthew, 1901. Late Palaeocene-Early Eocene; North America.
Pantolestes Cope, 1872. Middle Eocene; North America.
Cryptopithecus Schlosser, 1890. Late Eocene; Germany.
Opsiclaenodon Butler, 1946. Late Eocene; Britain.
Dyspterna Hopwood, 1927. Early Oligocene; Britain.
Androconus Quinet, 1965. Early Oligocene; Europe.
Chadronia Cook, 1954. Early Oligocene; North America.
Galethylax Gervais, 1848-52. Late Eocene; Europe.
Buxolestes Jaeger, 1970. Middle Eocene; Europe.

The above generic list follows that of Van Valen (1967) but with the tentative retention of *Opsiclaenodon* and *Bessoecetor* as distinct genera, and the addition of *Buxolestes*.

Simpson (1945) listed *Propalaeosinopa, Bessoecetor, Palaeosinopa,* and *Pantolestes*. Van Valen (1967) added a new genus *Pantomimus, Pagonomus, Cryptopithecus, Dyspterna, Androconus, Chadronia* and *Galethylax*. This latter problematical genus (discussion in Van Valen, 1966 : 73; 1967 : 227) was only provisionally referred to the family. Van Valen originally listed a new genus *Pantinomia* from the Middle Palaeocene of North America, as a pantolestid (1967 : 259) but in a later view (1967 : 225, footnote) referred it to the arctocyonids. In the same paper, Van Valen (1967) considered *Bessoecetor* as a synonym (tentative) of *Propalaeosinopa* and *Opsiclaenodon* as a synonym of *Cryptopithecus*, although Russell (*in* Russell, Louis & Poirier, 1966) retained *Bessoecetor* as a valid genus, into which he placed tentatively a new species, *B. levei*. More recently, Dr D. E. Russell (personal communication, 1971) has reaffirmed his belief in the validity of *Bessoecetor*. Russell (1964) in his type description of *Pagonomus* did not assign the genus to a subfamily; he noted resemblances of most of the teeth to the pentacodontine, *Aphronorus*. Additional confirmation of this view was given by a molarised P^4 tentatively referred to the genus by Russell (*in* Russell, Louis & Poirier, 1966). Van Valen (1967) considered the type of *Pagonomus* (an isolated M^2) as a pantolestine.

Genus ***OPSICLAENODON*** Butler, 1946

DIAGNOSIS. Lower molars with moderately elevated cusps, molars uncompressed antero-posteriorly. M_1 and M_2 very similar in size and structure, M_3 much smaller but quite similar structurally. Entoconid moderate-sized and distinct on all molars, hypoconid slightly larger. Hypoconulid of molars small but distinct, not extended posteriorly as a lobe on M_3. Upper molars moderately elongated transversely with rounded outlines; M^1 slightly smaller than M^2, M^3 markedly smaller; prominent hypocone in all molars; conules developed in all molars, situated close to metacone and paracone, the metaconule being larger than the paraconule. In M^2, conules well developed, but more rudimentary in M^1 and M^3. M^1 and M^2 parastylar region extended antero-externally, and metastylar region extended postero-externally, as prominent rounded lobes. No continuous cingulum round base of protocone.

TYPE SPECIES. *Opsiclaenodon major* (Lydekker, 1887). Lower Headon Beds (Mammal/Crocodile Bed), Hordle Cliff. The only known species.

REMARKS. Butler redescribed (1946) *Neurogymnurus major* Lydekker known only from fragmentary lower dentitions, as a new genus *Opsiclaenodon*. In his original description, Butler referred (1946 : 691) *Opsiclaenodon* to the Arctocyonidae, suggesting a relationship with *Dyspterna* and *Didymoconus*. McKenna (*in* Russell and McKenna, 1961 : 281, footnote) suggested that *Opsiclaenodon* was an oxyclaenine arctocyonid, with affinities to *Metachriacus*, *Mimotricentes* and *Spanoxyodon*. Russell (1964 : 193) observed that reference of *Opsiclaenodon* to the Oxyclaeninae was unlikely. Van Valen (1966) referred *Cryptopithecus* and *Dyspterna* to the Pantolestinae. He later added (1967) *Opsiclaenodon* as a synonym of *Cryptopithecus*. Restudy of Butler's material and examination of additional specimens, has confirmed Van Valen's view that *Opsiclaenodon* is a pantolestine. The type of *Cryptopithecus sideroolithicus* is a fragmentary left mandibular ramus with M_2–M_3 (Bayerische Staatssammlung für Paläontologie, Munich, No. A.S. (128) XI 1). Comparison with a cast of this specimen (kindly made available by Dr D. E. Russell) reveals reasonable structural differences (see below) and in the present work, the validity of Butler's genus is accepted provisionally, pending discovery of better more complete material of *Cryptopithecus*.

Isolated M^1 and M^2 (described below) referred to *Opsiclaenodon* show resemblances to the oxyclaenine arctocyonid, *Oxyclaenus*. However, in this genus, the internal margin of the upper molars is more angular and the hypocone is rudimentary; also the lower molars show important differences. The same specimens also show similarity within the arctocyonids to the triisodontine, *Goniacodon*, except for the poor hypocone development in the latter; M_1 and M_2 in these two genera also show similarities. However, these resemblances do not seem significant as *Opsiclaenodon* shows none of the peculiar adaptive features characteristic of the Triisodontinae.

Structurally, the referred upper molars of *Opsiclaenodon* are strikingly similar to some hyopsodontine condylarths such as *Haplaletes* and *Litomylus*. In the latter genus, however, the conules are stronger; tooth outlines are more angular; M^3 is triangular-shaped and lacks a hypocone. Also, P_4 has a metaconid and a small low paraconid. These characteristics (and those of the lower dentition such as P_4 with a metaconid and a small low paraconid) serve to exclude *Opsiclaenodon* from any close relationship with the Hyopsodontidae.

Amongst the described members of the Pantolestinae, *Propalaeosinopa* and *Bessoecetor* are easily distinguished from *Opsiclaenodon* by having slender elevated trigonid cusps; M_3 is much larger and bulbous and P_4 is very elongated with a strong anterior basal cusp and incipient basining of the talonid; M^1–M^2 are very slender and transversely elongated with a smaller hypocone and the outline of M_3 is quite different. In the European species provisionally referred to *Bessoecetor*, *B. levei*, the M^2 and M^3 are more slender and transversely elongated, with angular parastylar and metastylar areas; the lower molars are more angular with more elevated trigonids and the M_3 is longer antero-posteriorly than the other molars, with a posteriorly projecting hypoconulid. The upper molars of *Pantomimus* are more elongated transversely with prominent externally projecting metastylar and parastylar areas; a hypocone is absent. The M^2 (type) of *Pagomomus* is more elongated transversely with more elevated slender cusps and more angular metastylar and parastylar areas; the hypoconal area is more angular and posteriorly extended. In *Pantolestes* the upper molars are similar in shape to *Opsiclaenodon*, but the hypocone is very small and the metastylar and parastylar areas are rounded and less prominent; the lower canine is massive but lacks striations and a groove; the molar paraconid is vestigal and the hypoconulid is strong and posteriorly projecting, in M_3 forming an enlarged posterior lobe. In *Cryptopithecus*, the anterior margin of the molars is more rounded and blunt, with the M_1 paraconid smaller, less elevated and less separated from the protoconid; the trigonid is compressed antero-posteriorly with crowded elevated cusps; the M_1 metaconid is more massive and the talonid cusps are better developed than in *Opsiclaenodon* with a very strong hypoconid. The M_3 in *Palaeosinopa* is as large as M_2; the molar trigonids are slender and more elevated, especially M_3 and the antero-external cingulum is smaller. The upper molars are more elongated transversely with a small hypocone and the posterior mental foramen lies under M_2. *Buxolestes* has a relatively simple canine section; P_4 has a more elongated talonid; M_2 is more rectangular and antero-posteriorly compressed and M_3 is enlarged . In the upper molars of *Buxolestes*, M^2 is more elongated transversely with a less rounded outline and M^3 is triangular-shaped and only slightly reduced with a less developed parastylar area.

Apart from the closely related *Dyspterna* (see later discussion), *Opsiclaenodon* appears nearest structurally to the contemporaneous *Cryptopithecus*. The earlier European history of the family is poorly known and none of the described European species from the Palaeocene and Early-Middle Eocene appear to be closely related to *Opsiclaenodon* and *Cryptopithecus*. The Late Palaeocene and Early Eocene *Palaeosinopa*, however, seems to exhibit the basic dental structure from which *Opsiclaenodon* and *Cryptopithecus* could be derived.

Opsiclaenodon major (Lydekker, 1887)

(Text-figs 16–19)

1887 *Neurogymnurus major* Lydekker: 302
1967 *Cryptopithecus major* (Lydekker); Van Valen: 87

DIAGNOSIS. As for the genus.

LECTOTYPE. B.M. 29718a. Fragment of right mandibular ramus with P_4–M_3 and alveoli of the canine and P_2–P_3. Talonids badly worn. Lower Headon Beds (Mammal/Crocodile Bed), Hordle Cliff. Listed Lydekker, 1887 : 302. Figured Butler, 1946, fig. 1; fig. 2, (2), (9).

MATERIAL. All material is from the Lower Headon Beds (Mammal/Crocodile Bed), Hordle Cliff, except where otherwise stated.

B.M. 29718. Posterior fragment of left mandibular ramus with M_1–M_3. The coronoid, condyloid and angular processes preserved, though damaged. External surface embedded in matrix. Wear greater than lectotype. Listed Lydekker 1887 : 302. Figured Butler, 1946, fig. 1.

B.M. 36801. Fragment of right mandibular ramus with M_2–M_3. Listed Lydekker, 1887 : 303. Listed Butler, 1946 : 691.

B.M. 36802a. Fragment of right mandibular ramus with alveoli of M_1–M_3. Listed Butler, 1946 : 691.

B.M. 36803. Left mandibular ramus with P_2, M_3 the base of the canine and the alveoli of P_1 and P_3–M_2 Teeth unworn. Listed Lydekker, 1887 : 303. Figured Butler, 1946, fig. 1; fig. 2, (3), (4), (6), (7), (8), (10).

B.M. 36807. A crushed fragment of left mandibular ramus with M_2–M_3 and alveoli of P_4–M_1. External surface embedded in brown clayey sand matrix. Teeth unworn. Listed Lydekker, 1887 : 303. Figured Butler, 1946, fig. 2, (1), (5).

S.M. C53478. Isolated right M_1. Unworn. Damaged metaconid.

B.M. M12565b. Isolated right M_1. Unworn.

S.M. C30611. Fragment of left mandibular ramus with P_3–P_4 and alveoli of M_1, bases of alveoli of P_2 and the canine. Unworn.

S.M. C54162. Isolated teeth. All from Lower Headon Beds (Rodent Bed), Hordle Cliff.

a. Right P_2. Unworn.
b. Right M_2. Part worn.
c. Right M_2. Part worn.
d. Right M_2. Part worn.
e. Left M_1. Part worn.

B.M. 29863. Anterior fragment of left mandibular ramus with the canine, P_2–P_4, and alveolus of P_1. Tip of canine broken off. Symphysis preserved. Matrix of brown clayey sand.

B.M. M25094. Anterior fragment of right mandibular ramus with P_3 and alveoli of the canine, P_1, P_2, P_4 and M_1. Posterior part of symphysis preserved.

B.M. 25084. Isolated right lower canine. Tip damaged.

B.M. M25091. Isolated right M_3. Moderately worn.

S.M. C30713. Isolated right upper molar (M^2?). Unworn.

S.M. C30722. Isolated left upper molar (M^2?). Badly worn.

S.M. C9677. Isolated left upper molar (M^3?). Unworn.

S.M. C54163. Isolated right upper molar (M^1?). Moderately worn.

Lower Headon Beds (Rodent Bed), Hordle Cliff.

DESCRIPTION. The mandible is moderately elongated and stout with a slight anterior deepening. The symphysial surface (B.M. M25094, B.M. 36803 and B.M. 29863) is elongated and oval in outline, ending posteriorly below P_2. The posterior region of the mandible is preserved only in B.M. 29718: the condyle, situated above the level of the tooth row is damaged, but appears to have been transversely elongated. The angular and coronoid processes are separated from the condyle by fairly prominent notches. The masseteric fossa extends only slightly below the level of the tooth row; the mandibular foramen is situated similarly. The anterior mental foramen occurs below P_1/canine (B.M. 36803 and B.M. 29718a) or below P_1 (B.M. M25094 and B.M. 29863). The posterior mental foramen is also variably sited below P_4 (B.M. 36803 and B.M. 29718a) or M_1 (B.M. 36802a, B.M. 25094 and S.M. C30611). An additional small foramen occurs below P_3 (B.M. 29863 and B.M. 36803) or below P_2 (B.M. M25094).

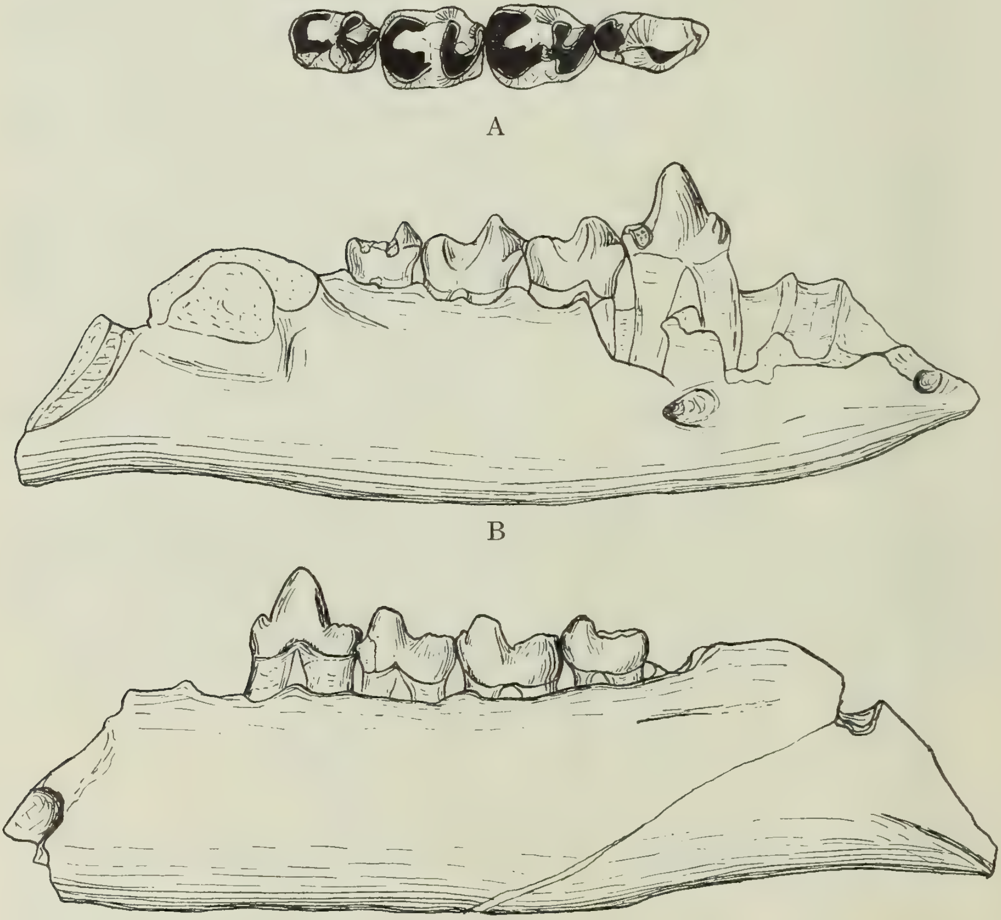

FIG. 16. *Opsiclaenodon major* (Lydekker, 1887). Fragmentary right mandibular ramus with P_4–M_3. Lectotype (B.M. 29718a) approx. ×3·5. Lower Headon Beds, Hordle Cliff. (A) Occlusal view. (B) External view. (C) Internal view.

The lower incisors are not known. The lower canine is known from B.M. 36803, B.M. 29863 and B.M. M25084. The upper half of the tooth is enamel covered; this enamel is wrinkled externally, forming regular striations. The upper half of the tooth is triangular in section with sharp postero-external, internal and antero-internal crests; the latter two crests bound a prominent groove. In B.M. 36803 and B.M. 29863 the groove, crests and enamel covering occur below alveolar level, but in these specimens, the tooth is incompletely erupted. These features are considered to occupy the upper half of the tooth, by analogy with material of *Dyspterna* (described later) where an almost identical tooth is fully developed and completely preserved. Butler, in his type description (1946 : 694) observed that the canine of B.M. 36803 was grooved and incompletely erupted, but did not record the curious external striations of the enamel and the enamel distribution. In B.M. 29718a the canine alveolus extends to the posterior end of the symphysis; in S.M. C30611 and B.M. M25094, it extends posterior to this.

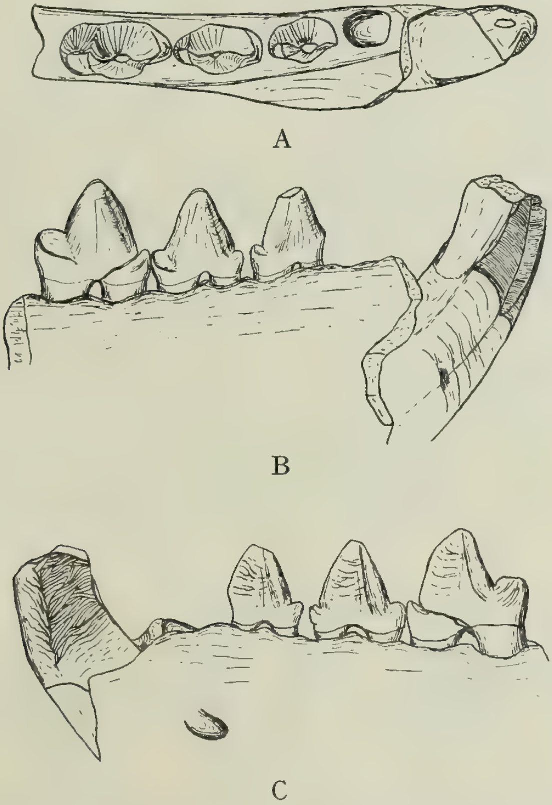

FIG. 17. *Opsiclaenodon major* (Lydekker, 1887). Fragmentary left mandibular ramus with C, P_2–P_4. B.M. 29863 ×3·5. Lower Headon Beds, Hordle Cliff. (A) Occlusal view. (B) Internal view. (C) External view.

P_1 from its alveolus (B.M. 36803, B.M. 29863 and B.M. M25094) was evidently small, single-rooted and placed immediately posterior to the canine. P_2 is preserved in B.M. 36803, S.M. C54162a and B.M. 29863; the tooth is double-rooted and has a slight forward inclination. From a single large anterior cusp, steep posterior and postero-internal crests fall to the antero-external and antero-internal extremities, respectively of a small slightly basined heel. An anterior crest from the main cusp curves internally at the anterior tooth margin forming a faint cingulum. On the antero-internal wall of the tooth, just posterior to the anterior crest, there is a vertical groove, similar to though less pronounced than that of the canine. Horizontal striations similar to those of the canine, are well developed externally on the main cusp in B.M. 29863 and S.M. C54162a, though less prominent on B.M. 36803. P_3 is known from S.M. C30611 and B.M. 29863; these specimens were not listed by Butler (1946) who described only alveoli of this tooth. The tooth is generally similar to P_2 but larger with a large crested main cusp. The anterior crest curves internally at the base of the antero-internal groove forming a very faint cingulum-like cuspule (S.M. C30611) or a strong low cusp (B.M. 29863). The posterior crest continues antero-posteriorly across the middle of the well developed heel. Externally, there is some development of irregular, subhorizontal enamel striations. P_4 (B.M. 29718a, S.M. C30611 and B.M. 29863) is very similar in structure to P_3 but much larger. The antero-internal groove is marked clearly on S.M. C30611 and B.M. 29863, but less prominent on B.M. 29718a. According to Butler (1946 : 695), the groove is absent in B.M. 29718a, the only specimen containing P_4 listed by him. The antero-posterior talonid crest in S.M. C30611 swells posteriorly to form a cusp; in B.M. 29863, the median region of the crest is raised as a distinct cusp. Two small internal cuspules occur on the talonid of B.M. 29718a; these are absent in the other specimens.

M_1–M_3 are structurally very similar with rounded trigonid and talonid margins; M_1 and M_2 are subequal; M_3 is markedly smaller. Identification of isolated teeth

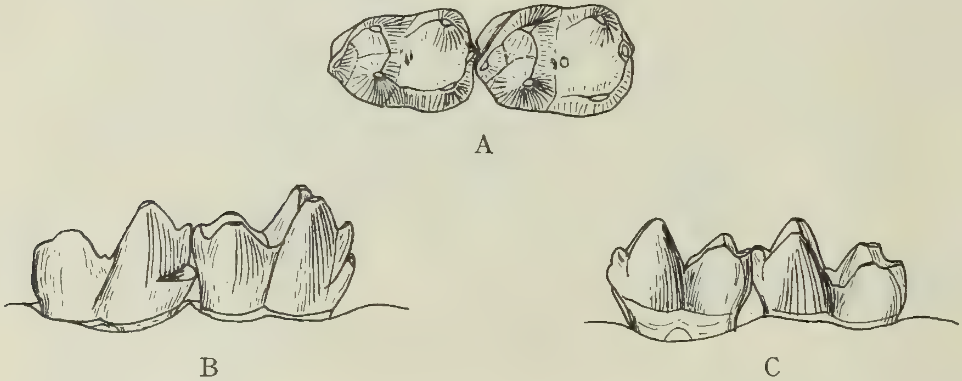

Fig. 18. *Opsiclaenodon major* (Lydekker, 1887). Composite right M_1–M_2 all approx. ×5. M_1 (B.M. M12565b) and M_2 (S.M.C 54162d). Lower Headon Beds, Hordle Cliff. (A) Occlusal view. (B) External view. (C) Internal view.

as M_1 or M_2 is uncertain; M_1 has been distinguished here by a slight anterior narrowing of the trigonid. The metaconid and protoconid are subequal (when unworn), opposite and transversely crested. The small though distinct low paraconid is median or slightly internal to the midline, forming the fairly sharp anterior apex of the tooth; a crest from this cusp meets the anterior protoconid crest. A fairly strong shelf-like antero-external cingulum is present. The hypoconid and entoconid are prominent and opposite, the hypoconid being slightly larger; each cusp is united to the posterior trigonid wall by sharp crests. The hypoconulid is small, though distinct; it is strongly posterior to the hypoconid and entoconid, and posteriorly projecting; the cusp is usually slightly external to the midline and is joined to the hypoconid and entoconid by low crests. This condition is seen in the M_3 of B.M. 36807, but this cusp in the M_3 of B.M. 29718 and B.M. 36803 is distinct and median. The talonid is strongly basined. Small accessory crests and cuspules are variably developed in the molars: in B.M. 36803, B.M. 36807 and B.M. M25091, a discontinuous crest swings obliquely down the posterior trigonid wall from the metaconid towards the crista obliqua; this cannot be distinguished in other specimens owing to excessive wear. On M_2 of B.M. 36807 and S.M. C54162d, there is a small cuspule in the middle of the talonid at the base of the posterior trigonid wall. This is absent in S.M. C54162b and S.M. C54162c. In other specimens wear is too great for this feature to be distinguished.

The upper teeth are known only in the isolated state. S.M. C30713 and S.M. C30722, almost identical structurally, are the largest teeth; these are considered as M^2. S.M. C54163 is somewhat smaller antero-posteriorly, showing several minor structural differences; this is tentatively considered as M^1. S.M. C9677, markedly smaller in length and width than the other teeth, probably represents M^3. M^2 is elongated transversely and has a rounded outline. The antero-internal crescentic protocone, the largest cusp, dominates the internal half of the tooth. The conical paracone is subequal in height with the protocone; the metacone is smaller. There is a strong shelf-like external and postero-external cingulum round the metacone base, ending externally as a small mesostyle, and a similar anterior cingulum round the base of the paracone (not present externally). The parastylar region is extended antero-externally, the metastylar region extended postero-externally, as rounded lobes. The sharp postero-externally trending protocone crest is interrupted just internal to

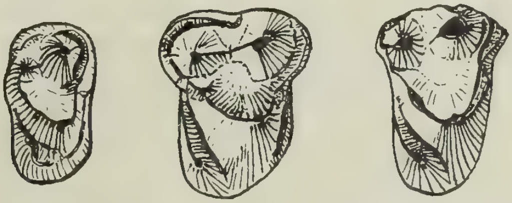

FIG. 19. *Opsiclaenodon major* (Lydekker, 1887). Occlusal view of composite M^1–M^3 ×5. Right M^1 (S.M. C54163), right M^2 (S.M. C30713) and left M^3 (S.M. C9677), drawing reversed. Lower Headon Beds, Hordle Cliff.

the metacone by a prominent metaconule. A smaller paraconule is similarly placed on the protocone crest just internal to the paracone. There is a small low anterior cingulum and a very strong shelf-like postero-internal cingulum which supports externally a very strong hypocone which is subequal in height with the metacone. S.M. C30722, a well worn M^2, has a more developed anterior cingulum. M^1 is basically similar to M^2 and although the tooth is more worn than M^2 (S.M C30713) and damaged externally, significant differences can still be recorded: the tooth is shorter antero-posteriorly than M^2. The hypocone and hypocone-cingulum are less developed; the metaconule is very small and the paraconule, just distinguishable on the slightly worn crest must have been very rudimentary on the unworn tooth. The postero-external cingulum round the base of the metacone is absent and there is only a trace of the antero-internal cingulum. M^3 is basically similar to the other molars but much smaller and compressed antero-posteriorly. The metaconule is very small, merging with the antero-external cingulum and an internal paracone crest. The antero-external trending protocone crest joins the paracone; a small swelling on this crest just internal to the paracone indicates a rudimentary paraconule. A small postero-external cingulum is present, but not round the metacone base as in M^1 and M^2; this latter cusp, slightly smaller than the hypocone, is more antero-internal than in M^1 and M^2.

REMARKS. There is considerable variation in the depth of the mandible: B.M. 29718a is greatest, B.M. 29718 intermediate, and B.M. 36803 smallest in size. B.M. 36803 has unworn teeth and an incompletely erupted canine, indicating derivation from a very young individual. This suggests that the variation in mandible depth is, at least in part, related to individual age differences. There are slight variations in the positions of the mental foramina; in the degree of prominence of the antero-

TABLE 10

Measurements (in mm) of *Opsiclaenodon major*

	P_2		P_3		P_4		M_1		M_2		M_3	
	a-p	trs	a-p	trs	a-p	trs	a-p	trs	a-p	trs	a-p	trs
B.M. 29718	—	—	—	—	—	—	4·1	3·3	4·2	3·3	3·7	2·8
B.M. 29718a	—	—	—	—	4·5	2·3	4·0	3·4	4·1	3·3	3·4	2·6
B.M. 36807	—	—	—	—	—	—	—	—	4·4	3·3	3·5	2·6
B.M. 36802	—	—	—	—	—	—	—	—	4·3	2·9	3·2	2·3
B.M. M12565b	—	—	—	—	—	—	4·2	3·2	—	—	—	—
B.M. 36803	3·1	1·8	—	—	—	—	—	—	—	—	3·5	2·6
B.M. 29863	3·0	1·8	3·6	2·0	4·5	2·4	—	—	—	—	—	—
B.M. M25094	—	—	3·6	2·0	—	—	—	—	—	—	—	—
B.M. M25091	—	—	—	—	—	—	—	—	—	—	3·2	2·6
S.M. C53478	—	—	—	—	—	—	3·8	3·0	—	—	—	—
S.M. C54162a	3·0	1·7	—	—	—	—	—	—	—	—	—	—
,, ,, b	—	—	—	—	—	—	—	—	4·4	3·2	—	—
,, ,, c	—	—	—	—	—	—	—	—	4·1	3·2	—	—
,, ,, d	—	—	—	—	—	—	—	—	4·4	3·4	—	—
,, ,, e	—	—	—	—	—	—	4·3	3·2	—	—	—	—
S.M. C30611	—	—	3·7	1·9	4·2	2·4	—	—	—	—	—	—

internal groove and antero-external enamel striations in the premolars, and in the development of accessory cuspules. These have been considered in the preceding description.

Genus ***DYSPTERNA*** Hopwood, 1927

DIAGNOSIS. Lower molars with low blunt cusps, M_3 trigonid rather compressed antero-posteriorly. M_1 and M_3 probably subequal in size, M_2 larger. Entoconid of molars vestigial or absent with postero-internal talonid margin raised as a crest, hypoconid large. Hypoconulid of molars median and small to vestigial.

TYPE SPECIES. *Dyspterna woodi* Hopwood, 1927. Early Oligocene ('Sannoisian'), Yarmouth, Isle of Wight.

REMARKS. The genus was originally based by Hopwood on a single specimen, from the Lower Hamstead Beds, a very fragmentary worn and damaged mandibular ramus with M_2–M_3 (B.M. M13125), provisionally placed in the Oxyclaeninae. Three years later, Dal Piaz described (1930) a maxillary fragment with P^4–M^3 which he tentatively referred to Hopwood's species. This specimen was removed by Van Valen (1966 : 88) from *Opsiclaenodon* as the type of a new apheliscine, *Epapheliscus italicus* Van Valen, 1966. Dal Piaz also described a new species (1930 : 13) which he tentatively referred to the genus as ?*Dyspterna helbingi*; the holotype (and only known specimen) is a fragmentary left maxilla with P^3 and the roots of P^4–M^3. Recently, Van Valen has observed (1966 : 88) that from the published figure and description, the affinities of this specimen cannot be determined.

In his redescription of *Neurogymnurus major* as *Opsiclaenodon major*, Butler suggested (1946 : 698) a possible relationship with *Dyspterna woodi*. The genus was not listed by Simpson (1945) being based on inadequate material, and McKenna stated (*in* Russell & McKenna, 1961 : 281, footnote 3) that *Dyspterna* constitutes practically a *nomen dubium*. Van Valen (1966 and 1967) referred *Dyspterna* to the Pantolestidae.

In the present work, material collected fairly recently from the Upper Headon Beds has been referred to *Dyspterna* (on the basis of molar structure) as a new species. The anterior lower dentition of this species of *Dyspterna* is strikingly similar to that of *Opsiclaenodon* and the two genera appear to be closely related, thus supporting Butler's original view.

Opsiclaenodon is distinguished generically from *Dyspterna* by the uncompressed M_3 trigonid; the molar entoconid is strongly developed; the hypoconulid is well defined and the cusps are more trenchant and separated. The prominent hypoconid and vestigial or absent entoconid sharply distinguishes *Dyspterna* from all other pantolestines. These and other specialised features could have arisen by modification of a dental structure similar to that of *Opsiclaenodon*.

Van Valen has stated (1967 : 227) that *Opsiclaenodon* could be directly ancestral to *Dyspterna*. This possibility is precluded by the contemporaneous occurrence of *Dyspterna hopwoodi* sp. nov. and *Opsiclaenodon major* in the Headon Beds; both genera were probably derived from an earlier common ancestry, perhaps in the Middle Eocene.

Dyspterna hopwoodi sp. nov.

(Text-figs 20, 21)

ETYMOLOGY. After A. T. Hopwood.

DIAGNOSIS. M_1 and M_3 hypoconid large, entoconid and hypoconulid vestigial, appearing as small swellings on postero-internal marginal crest. Crista obliqua in M_1 and M_3 directed anteriorly to base of protoconid. M_3 trigonid more compressed antero-posteriorly than in *D. woodi*, with the small paraconid strongly antero-internal in position, close to metaconid; M_3 hypoconulid vestigial. Sharp condyloid and coronoid crests bordering deep masseteric fossa.

HOLOTYPE. B.M. M26052. Right mandibular ramus with the canine, P_2–P_4 and M_3, and alveoli of I_1–I_3, P_1 and M_1–M_2. Symphysis and posterior region of mandible are preserved. Slightly worn dentition. Upper Headon Beds (Lignite Bed), Headon Hill.

PARATYPES. B.M. M26053. Isolated right M_1. Slightly worn. Upper Headon Beds (Lignite Bed), Headon Hill.

B.M. M26054. Isolated right P_1. Unworn. Upper Headon Beds (Lignite Bed), Headon Hill.

DESCRIPTION. The mandible is moderately stout with a slight anterior deepening as in *Opsiclaenodon*. The symphysis is elongated and rectangular in outline, ending posteriorly under P_2 and inclined at about 45° to the level of the tooth row. The posterior region of the mandible is complete in the holotype, except for the condyle which lay just above the level of the tooth row. The coronoid process is well developed and massive, the anterior edge rising steeply from the tooth row level. The notch between the condyle and the coronoid is hardly perceptible; this is in contrast to *Opsiclaenodon*, where it appears to have been more developed. The angular is fairly prominent and well separated from the condyle; the lower edge is deflected internally as a small flange. The mandibular foramen is situated just below alveolar level; the ridge above this running from the condyle to a position below M_3 is more prominent than in *Opsiclaenodon*. The anterior mental foramen is sited below the canine/P_1, the posterior mental foramen below M_1.

The bases of the alveoli of I_1–I_3 indicate that these teeth were closely crowded and situated immediately anterior to the canine. The canine is almost identical to that of *Opsiclaenodon major* with the upper half of the tooth enamel covered; externally the enamel is wrinkled, forming regular striations. The upper half of the tooth is triangular-shaped with sharp antero-internal, internal and postero-external crests, and a prominent deep antero-internal groove. The groove and crests are confined mainly to the enamel-covered upper half of the tooth. Below this level, the crests become rounded but the groove, in contrast to *Opsiclaenodon major* is continued to alveolar level as a distinct but rounded constriction. From the alveolus in the holotype, it appears that P_1 was a little separated from the canine; the tooth (B.M. M26054) is single-rooted with a main central cusp and a small postero-internal heel. The cusp is crested anteriorly, postero-internally and posteriorly. There are small but distinct antero-internal and postero-external cingula and a cingulum trace antero-externally. A rudimentary antero-internal groove is present.

P_2 is slightly larger than P_1 and double-rooted. There are no antero-external and postero-external cingula; otherwise the tooth is structurally nearly identical to P_1. There is the suggestion of a slight antero-internal groove. P_3 is identical to P_2, except for a larger size and a slightly stronger cusp-like antero-internal cingulum. There is a trace of an antero-internal groove. P_4 is structurally quite similar to P_3 but much larger. The sharp anteriorly crested main cusp falls to a prominent low anterior cusp; this latter cusp is larger than that of *Opsiclaenodon* and the tooth is generally more pointed. There are small antero-external and antero-internal cingula. The antero-posterior talonid crest ends posteriorly in a small cusp. There is a slight antero-internal groove.

It is difficult to estimate reliably the relative sizes of M_1 and M_2 from the alveoli in the holotype of *D. hopwoodi* because of mandible damage. By comparison with the holotype of *D. woodi* (about the same size as *D. hopwoodi*) where M_3 is smaller than

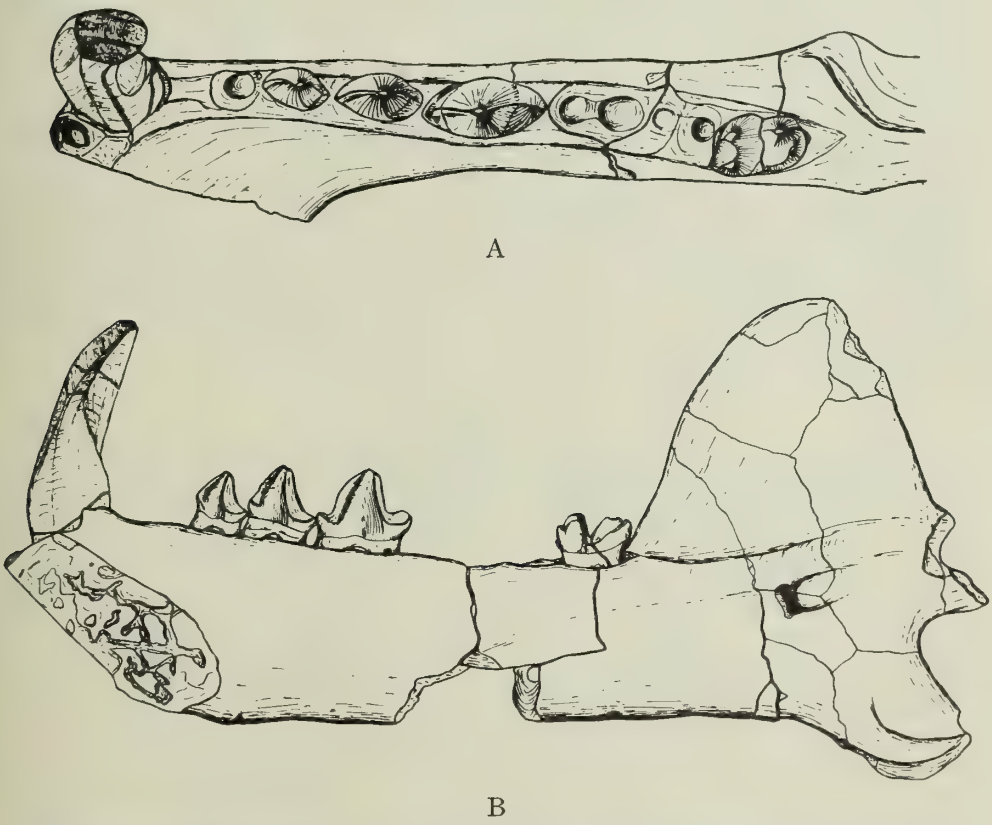

FIG. 20. *Dyspterna hopwoodi* sp. nov. Right mandibular ramus with C, P_2–P_4 and M_3. Holotype (B.M. M26052). Upper Headon Beds, Headon Hill. (A) Occlusal view ×2·5. (B) Internal view ×2.

M_2, it has been concluded that an isolated molar (paratype) of *D. hopwoodi* is best considered as M_1. This latter tooth is elongated with a rounded margin. The protoconid and metaconid are subequal, opposite and transversely crested. The small but distinct low median paraconid forms the sharp anterior apex of the tooth. There is a moderately strong antero-external cingulum and a smaller antero-internal cingulum. The entoconid and hypoconid are vestigial, appearing as small swellings on a low curved crest which forms the postero-internal talonid margin. The median hypoconulid projects slightly posteriorly; the entoconid and hypoconid are opposite each other. The talonid is slightly basined. M_3 is almost the same length as M_1, with a subequal and opposite protoconid and metaconid. The smaller paraconid is strongly internal and anterior to the metaconid; the trigonid appears antero-posteriorly compressed. The almost straight antero-external trigonid margin is formed by a paraconid and protoconid crest. There is a small antero-external cingulum but the antero-internal cingulum is absent. The vestigial hypoconulid is represented by a minute rounded median lobe which is posteriorly projecting and separated from the larger hypoconid. The entoconid is vestigial; a low rounded crest runs anteriorly from the hypoconulid-lobe, forming the postero-internal tooth margin. The talonid is only very slightly basined.

Remarks. In the canine of the holotype (B.M. M26052) distinct wear facets are visible: part of the postero-external face has been gauged away by the upper canine in occlusion, to form above alveolar level, a prominent oblique baso-exteriorly directed shelf. Wear has taken place along the whole vertical length of the tooth from the tip to this shelf, but becomes progressively greater towards this latter position; presumably slight wear took place near the canine tip when the tooth was partially erupted (compare *Opsiclaenodon major*, B.M. 29863). Anteriorly and basally to the prominent groove, there is a shallow vertical oval facet, produced probably by friction against one of the upper incisors.

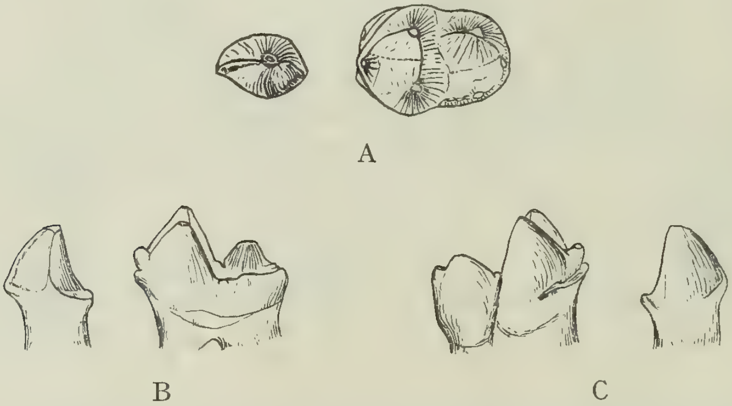

Fig. 21. *Dyspterna hopwoodi* sp. nov. Right P_1 (B.M. M26054) and right M_2 (B.M. M26053). Both ×4. Upper Headon Beds, Headon Hill. (A) Occlusal view. (B) Internal view. (C) External view.

The antero-internal groove does not show any signs of wear; the bordering crests are very sharp and quite unworn. The same situation exists in the closely similar canine of *Opsiclaenodon major*. As Butler noted (1946 : 695), a similar unworn groove occurs on the lower canine of *Nasua*, a recent procyonid. No information has been found about the significance of this groove in *Nasua*. On the available evidence, the structure in all three genera would appear to be non-functional, at least in occlusion.

In molar structure, *D. hopwoodi* is closely related to the type species, *D. woodi* and may be ancestral to the latter. *D. hopwoodi* sp. nov. appears specifically distinct on the basis of the following differences: in *D. woodi*, the hypoconid crest is directed antero-internally to meet the base of the metaconid, in M_3 running up the posterior wall of the metaconid; the cingula are relatively larger and more shelf-like; the M_3 trigonid is less compressed antero-posteriorly with the paraconid slightly more median; the hypoconulid appears to have been relatively larger, and the coronoid and condyloid processes are lower and more rounded, enclosing a shallower masseteric fossa. More detailed comparison is not possible because of the poor preservation of the holotype of *D. woodi*.

TABLE 11

Measurements (in mm) of *Dyspterna hopwoodi*

	P_1		P_2		P_3		P_4		M_1		M_2		M_3	
	a-p	trs	a-p	trs	a-p	trs	a-p	trs	a-p	trs	a-p	trs	a-p	trs
B.M. M26052	—	—	3·6	2·3	4·7	2·8	6·6	3·3	—	—	—	—	5·0	3·6
B.M. M26053	—	—	—	—	—	—	—	—	5·4	3·7	—	—	—	—
B.M. M26054	3·4	2·9	—	—	—	—	—	—	—	—	—	—	—	—

Family **APATEMYIDAE** Matthew, 1909

DIAGNOSIS. Genera with a reduced dental formula—probably $\frac{2}{1}, \frac{0}{0}, \frac{2}{2}, \frac{3}{3}$. Jaw deep and stout in proportion to molars, with posterior mental foramen below M_1 or M_2. Marked soricid-like development of lower incisors, the roots of which terminate below M_3. P_3 blade-like and single-rooted. Molars in early forms trenchant; more typically, bunodont and primate-like in appearance. P^3–P^4 double-rooted and unicuspid. Upper molars relatively elongated antero-posteriorly and broadly expanded postero-internally with a well developed hypocone, but lacking a mesostyle. Lower molars, except for M_3, have a simple talonid but the trigonid, particularly in M_2–M_3 shows a distinctive parallelogram arrangement of cusps and crests. (Mainly after Gazin, 1958).

REMARKS. Of the seven genera assigned to the family, five are known from North America and two from Europe:

Jepsenella Simpson, 1940. Middle Palaeocene; North America.
Labidolemur Matthew & Granger, 1921. Late Palaeocene; North America.
Apatemys Marsh, 1872. Early-Late Eocene; North America.

Stehlinella Matthew, 1929. Late Eocene; North America.
Sinclairella Jepsen, 1934. Early-Middle Oligocene; North America.
Eochiromys Teilhard de Chardin, 1927. Early Eocene; Belgium.
Heterohyus Gervais, 1848-52. Middle-Early Eocene; Europe.

Van Valen (1967) considered *Teilhardella* Jepsen, 1930 was invalid and included it within *Apatemys*. In addition to the above generic list, McKenna (1963 : 30) suggested that *Unuchinia* Simpson, 1937, previously placed *incertae sedis* in the Insectivora, might be an apatemyid. More recently, Van Valen (1967) formerly erected a new subfamily Unuchiniinae Van Valen & McKenna, for the reception of *Unuchinia*.

Stehlinella is known from the anterior portion of the skull with part of the upper dentition and an almost complete mandibular ramus lacking only P_4. *Sinclairella* is known from a complete but crushed skull with part of the upper dentition and a mandibular ramus lacking P_3–P_4 and M_1. The remaining six genera are based on fragmentary mandibles, although *Heterohyus* is known also from a palatal fragment.

Owing to incomplete material and the comparative rarity of specimens, classification is very tentative. Some genera are probably composite but better material is needed before significant advances can be made.

The family has oscillated between Primates and Insectivora for many years. The most recent detailed work on the affinities of this problematical group is McKenna (1963). From a consideration of molar structure in the earliest genera, McKenna referred the family to the Insectivora; this view, followed by Van Valen (1967) is adopted here.

Genus ***HETEROHYUS*** Gervais, 1848–52

Diagnosis. Usually single mental foramen below M_2; fossa below P_4 generally reduced. Enamel covering lower incisors extends into alveolus but does not completely coat the crown; P_4 generally reduced; M_3 talonid usually strongly elongated and M_3 posterior trigonid wall usually oblique to longitudinal axis of tooth.

Type species. *Heterohyus armatus* Gervais, 1848-52. Middle Eocene (Early Lutetian); Bouxwiller, France.

Remarks. Distinguished from the other genera as follows: *Jepsenella* shows only incipient development of apatemyid characteristics; in *Eochiromys* and *Labidolemur* the incisor crown is completely covered by enamel. These genera and all other apatemyids possess either a little-elongated M_3 talonid or lower molars with a transverse posterior trigonid wall.

Five species have been distinguished:

H. armatus Gervais, 1848-52, pl. 35, fig. 14. Middle Eocene (Early Lutetian); France.

H. quercyi (Filhol, 1880), p. 174, figs 1–3. Late Eocene (Early Ludian, Quercy Phosphorites); France.

H. nanus Teilhard de Chardin, 1922, p. 93, fig. 41; pl. 4, fig. 21. Late Eocene (Early Ludian, Quercy Phosphorites); France.

H. europaeus (Rütimeyer, 1890), p. 346, figs 1–2. Middle Eocene (Early-Middle Lutetian); Switzerland.

H.heufelderi Heller, 1930, p. 32, pl. 5, fig. 4. Middle Eocene (Lutetian); Germany.

The most complete species, *H. quercyi*, is based on a crushed skull and almost complete upper dentition and a fragmentary mandibular ramus; *H. nanus* and *H. armatus* are based on mandibular fragments, *H. heufelderi* on a complete lower dentition. The type of *H. armatus* (the type species) was not located by Teilhard de Chardin (1922 : 89) and here, is considered to be lost.

Stehlin (1916 : 1462) erected the genus *Heterochiromys* for two species from Egerkingen: *H. gracilis* known from mandibular rami lacking teeth and isolated incisors, and *H. fortis* based on isolated incisors. It is highly probable, as suggested by Teilhard de Chardin (1922 : 92), that *Heterochiromys gracilis* Stehlin is synonymous with *Heterohyus quercyi* (Filhol) and *Heterochiromys fortis* Stehlin, is synonymous with *Heterohyus armatus* Gervais. Stehlin (1916 : 1434) also placed several mandibular rami lacking teeth, and isolated incisors from Egerkingen in a new genus and species, *Amphichiromys europaeus*. This was based on minor differences in the incisors. Isolated lower molars tentatively assigned by Stehlin to this genus are of characteristic heterohyid type and apparently do not warrant generic separation. The genus is considered synonymous with *Heterohyus*.

The generic diagnosis is unsatisfactory and probably, *Heterohyus* is a composite genus. *H. nanus* does not fit well into this diagnosis and appears to be indistinguishable from *Apatemys bellus*. American material has not been examined, so this view is only tentative.

The material described below, constitutes the first record of an apatemyid from the Tertiary of Britain.

Heterohyus sp.

(Text-fig. 22)

MATERIAL. S.M. C54172. Isolated left M3. Moderately worn. Lower Headon Beds (Rodent Bed), Hordle Cliff.

DESCRIPTION. This strongly elongated tooth is composed mainly of a gently basined talonid, the latter being $2\frac{1}{2}\times$ the length of the trigonid. The trigonid is wider than the talonid and externally projecting. The low blunt cusps and crests of the trigonid exhibit a distinctive parallelogram arrangement.

The metaconid and paraconid are almost equal in size, the antero-internal paraconid being directly anterior to the metaconid; these cusps are united by a massive antero-posterior crest. The smaller protoconid is moderately separated from the metaconid and paraconid, and more anteriorly placed in relation to the metaconid; the posterior trigonid wall is thus markedly oblique to the longitudinal axis of the tooth. From the paraconid a small low crest runs parallel to the posterior trigonid wall, forming the oblique anterior tooth margin. The antero-external extremity of the tooth, directly anterior to the protoconid, is sharp and acute-angled; here, the crest is very faint and low.

The talonid basin is bounded externally and internally by rounded fairly strong crests which are almost parallel. The higher crista obliqua meets the posterior trigonid wall midway between the metaconid and protoconid; the internal crest is continued faintly up the posterior wall of the metaconid. The internal talonid margin is damaged; it may have curved out internally, with a more rounded outline than the external margin. Around the posterior edge of this damaged area is the possible trace of a small entoconid. From this position, the straight talonid margin runs to a relatively high rounded externally shifted hypoconulid-lobe. From the entoconid, a minute crest dilates as it curves round to meet a prominent hypoconulid, in the anterior part of the hypoconulid-lobe. No hypoconid is distinguishable, although the tooth is damaged anterior to the hypoconulid; a small cusp may have been present.

The total antero-posterior length of M_3 is 5·8 mm; the trigonid length is 1·6 mm, that of the talonid 3·7 mm. The trigonid transverse width is 2·9 mm, the talonid width is 2·2 mm.

REMARKS. This specimen is distinguished from the M_3 of known species as follows: *H. nanus* is much smaller with a short talonid and a slightly oblique trigonid; *H. quercyi* is much smaller with a slightly oblique trigonid; *H. europaeus* is larger with a slightly oblique trigonid; *H. heufelderi* is smaller with a relatively shorter talonid and in *H. armatus* the talonid is less elongated and wider transversely than the trigonid. Also, the tooth outline in all the above is more prominently rounded.

The Headon Beds specimen appears closest to *H. armatus*. However, little is known about variation within the genus; the known species are restricted to the

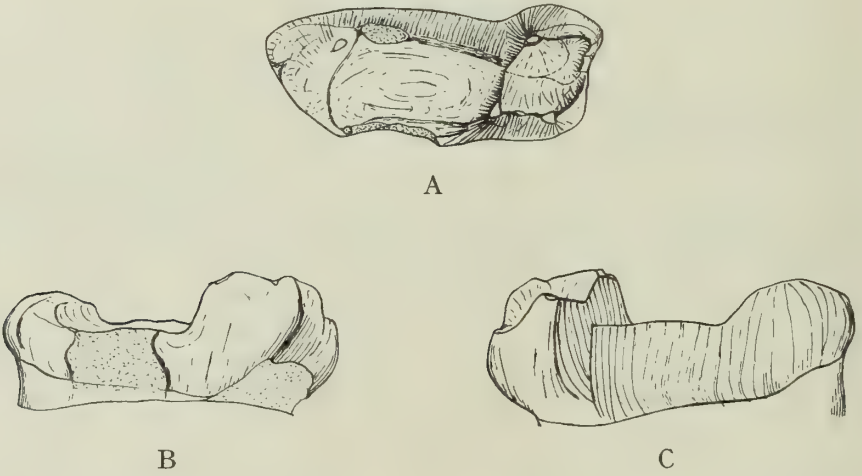

FIG. 22. *Heterohyus* sp. Left M_3. S.M. C54172 approx. ×8. Lower Headon Beds, Hordle Cliff. (A) Occlusal view. (B) Internal view. (C) External view.

Lutetian and Early Ludian and the genus already may be oversplit. S.M. C54172 could represent a distinct new species but better material is needed. At present the specimen seems best recorded as *Heterohyus* sp.

TABLE 12

Measurements (in mm) of M_3 of *Heterohyus* species

	Total a-p length	Ratio of trigonid length to talonid length	Angle between posterior wall of trigonid and longitudinal axis
H. heufelderi (*ex* Heller, 1930)	4·0	—	—
H. quercyi (*ex* Teilhard de Chardin, 1922)	3·9	1 : 2½	100°
H. nanus (*ex* Teilhard de Chardin, 1922)	2·5	1 : 1½	105°
H. armatus (*ex* Gervais, 1848-52)	7·0	1 : 2	130°
H. europaeus (*ex* Stehlin, 1916)	9·0	1 : 2½	100°
H. sp. (S.M. C54172)	5·8	1 : 2½	120°

Order PRIMATES

Family **ADAPIDAE** Trouessart, 1879

DIAGNOSIS. Dental series usually continuous—no marked diastema. Incisors typically wide-crowned and trenchant; upper canines straight, lower canines short, subpremolariform. Upper molars tritubercular or quadritubercular with a large V-shaped protocone; small but true hypocone derived from posterior cingulum; mesostyle usually absent. Paraconid absent or much reduced on lower molars; entoconid retarded; hypoconulid absent or rudimentary except on M_3. Mandible generally short and stout with a greatly expanded angular and a high recurved coronoid process. Condyle elongated transversely and relatively flattened. Skull usually with high sagittal and lambdoidal crests. Small ovoid braincase. Prominent heavy facial region. (after Hill, 1953).

REMARKS. Simons (1962) presented a revised classification of European Eocene primates. This revision, together with Gazin's revival (Gazin, 1958 : 31) of the family Notharctidae Trouessart, 1879, has significantly altered Simpson's classification of 1945. The generic list follows Simons (1962) with the addition of *Lantianus* Chow, 1964.

Adapis Cuvier, 1822. Middle-Late Eocene; France, Britain, Switzerland.
Pronycticebus Grandidier, 1904. Late Eocene; France.
Anchomomys Stehlin, 1916. Middle-Late Eocene; France, Switzerland.
Caenopithecus Rütimeyer, 1862. Middle Eocene; Switzerland.
Protoadapis Lemoine, 1878. Early-Late Eocene; France, Germany.
Gesneropithex Hürzeler, 1946. Late Eocene; Switzerland.
Lantianus Chow, 1964. ?Late Eocene; China.

In addition to *Caenopithecus*, Simpson, (1945) considered two further genera as Adapidae *incertae sedis*: *Aphanolemur* Granger & Gregory, 1917 and *Amphilemur* Heller, 1935. *Aphanolemur* is now believed to be a synonym of *Smilodectes* Wortman, 1903, a notharctid (Gazin, 1958 : 30). *Amphilemur* has been considered by McKenna (1960 : 58) as an erinaceoid insectivore. More recently, Simon's generic list has been accepted by McKenna (1967) and Russell, Louis & Savage (1967) although the latter authors regarded reference of *Gesneropithex* as provisional and tentatively added *Periconodon* Stehlin, placed by Simons (1962) and McKenna (1967) in the Omomyidae.

Genus **ADAPIS** Cuvier, 1822

SYNONOMY. See Hill, 1953 : 464.

DIAGNOSIS. Mandible has a greatly expanded angular process; coronoid process separated from condyle by a fairly shallow notch. P_1 present, small in size; P_4 submolariform but cusps variably developed; M_1 and M_2 similar to P_4; M_3 considerably elongated by hypoconulid which is not isolated distinctly as a third lobe; metastylid present in later species. P^1 present, small in size; P^4 molariform with a bicusped ectoloph. Upper molars lack mesostyle; hypocone not strongly developed, absent in M^3; metaconule rudimentary or absent; strong external cingulum; internal cingulum continuous.

TYPE SPECIES. *Adapis parisiensis* (Blainville, 1841). Late Eocene (Late Ludian); France.

REMARKS. *Anchomomys*, *Pronycticebus*, and *Caenopithecus* differ from *Adapis* by having the M_3 hypoconulid more distinctly separated as a lobe and by lacking the bicusped ectoloph of P_4 and the continuous internal upper molar cingulum. *Caenopithecus* is further distinguished by lacking P^1 and having a mesostyle. In *Protoadapis* P_2 is much smaller than P_3 and the molar paraconids extend more internally. *Gesneropithex* has a median paraconid; the metaconid—protoconid crest is perpendicular to the longitudinal axis of the tooth and the M_2 trigonid is compressed antero-posteriorly.

The following species are referred to *Adapis*:

A. parisiensis (Blainville, 1841), p. 112, pl. 9. Late Eocene (Bartonian-Late Ludian); France.

A. magnus Filhol, 1874, p. 11, pl. 8, figs 9–12. Late Eocene (Bartonian-Early Ludian); France, Britain.

A. ruetimeyeri Stehlin, 1912, p. 1261, pl. 21, figs 5, 8, 12, 14. pl. 22, figs 17–19. Middle Eocene (Late Lutetian); Switzerland.

A. sciureus Stehlin, 1916, p. 1514, text-figs 368–370, pl. 22, fig. 5. Middle Eocene (Early Lutetian); Switzerland.

A. priscus Stehlin, 1916, p. 1511, text-figs 366–367. Middle Eocene (Early Lutetian); Switzerland.

Simons (1962) observed that the holotype of *Adapis minimus* Heller, 1930, is indeterminate owing to removal of enamel by post-mortem chemical absorption.

Adapis magnus Filhol, 1874

(Pl. 1; Pl. 2, fig. 1)

DIAGNOSIS. Large size. Molars moderately elongated; metastylid developed. Upper canines large with grooved crown; P^3 transversely elongated with prominent internal cingulum and talonid.

HOLOTYPE. Fairly complete skull lacking the incisors and canines of both sides, left P^1–P^2 and M^3. ?Late Eocene/Early Oligocene (Quercy Phosphorites); Raynal, France. Described and figured, Filhol, 1874, p. 11, pl. 8, figs 9–12. Specimen not located.

MATERIAL. All specimens from the Lower Headon Beds (Mammal/Crocodile Bed), Hordle Cliff.

B.M. 30323. Fragment of right mandibular ramus with M_1–M_3. Very slightly worn. Brown shelly sand matrix. Listed, Lydekker, 1885a : 263.

B.M. 30856. Fragment of right mandibular ramus with M_2–M_3. Moderately worn. Brown sand matrix. Listed, Lydekker, 1885a : 263.

B.M. 29864. Fragment of right mandibular ramus with P_4–P_1, and posterior root of P_3. Moderately worn. Listed, Lydekker, 1885a : 263.

B.M. 29741. Fragment of left mandibular ramus with P_4, M_3, roots of P_3 and part of the canine. Teeth and alveoli of P_1–P_2 are badly damaged. External surface embedded in brown clayey sand matrix. Listed, Lydekker, 1885a : 263.

B.M. M10260. Fragment of left mandibular ramus with P_3–M_2 and alveoli of M_3. Fairly well worn.

B.M. M10269. Fragment of right mandibular ramus with P_4–M_2. Teeth unworn.

B.M. M10267 (3). Fragment of left mandibular ramus with M_1–M_2. Moderately worn.

D.M.S.W. M556 (41). Fragment of left mandibular ramus with P_4–M_2.

B.M. M26057 (1). Right M_2.

(2). Right M_1. Both teeth slightly worn. Wear and preservation indicates probable derivation from same individual.

B.M. M20560. Right M_2. Badly worn.

B.M. M25093. Left M_3. Badly damaged.

S.M. C30680. Fragment of right mandibular ramus with M_1–M_2. Slightly worn.

S.M. C53483. Left M_3. Unworn

S.M. C53477. Right M_3. Moderately worn.

S.M. C54221. Right M_2. Unworn.

S.M. C30659. Right M_1. Moderately worn.

S.M. C30660. Right M_1. Well worn.

S.M. C30656. Left M_2. Well worn.

S.M. C30658. Right M_2. Well worn.

S.M. C30657. Right M_1. Well worn.

S.M. C31345. Left M_2 (?). Well worn and badly damaged.

B.M. M3572. Fragment of left maxilla with left half of palate and P^2–P^3, M^1–M^3 and alveoli of the canine and P^1. P^2 is damaged. Teeth unworn. Listed, Lydekker, 1887 : 299.

B.M. M10261 (1). Left upper molar (M^2?). Moderately worn.
(2). Right upper molar (M^2?). Moderately worn.
(3). Upper molar. Moderately worn but badly damaged.
B.M. M20560 (1). Left upper molar (M^2?). Slightly worn.
(2). Left P^4. Moderately worn.
S.M. C53484. Left upper molar (M^3?). Unworn.
S.M. C30661. Right upper molar (M^2?). Slightly worn.
S.M. C30662. Right upper molar (M^1?). Slightly worn. Probably from same individual as S.M. C30661.
B.M. M25098. Right upper molar (M^2?). Unworn.
B.M. 25092. Right upper molar (M^1?). Moderately worn.
S.M. C53479. Left upper molar (M^3?). Moderately worn.
B.M. 12564 (1). Left upper molar (M^2?). Slightly worn.
(2). Right P^4. Moderately worn.
S.M. C30681. Right upper molar (M^3?). Well worn.
S.M. C30679. Left upper molar (M^1?). Badly worn.
S.M. C30673. Left upper molar (M^2?). Unworn.
S.M. C30674. Left upper molar (M^1?). Slightly worn. Probably from same individual as S.M. C30673.
S.M. C30678. Left P^4. Moderately worn.
S.M. C30675. Left upper molar (M^2?). Badly worn.
S.M. C30676. Right upper molar (M^2?). Slightly worn.
S.M. C30677. Fragment of upper molar.
B.M. 30346a. Listed, Lydekker, 1885a : 263.
(1) Right upper molar (M^2?). Slightly worn.
(2) Left upper molar (M^3?). Slightly worn. Probably from same individual as B.M. 30346a (1).
(3) Left P^4. Unworn.
(4) Left upper molar (M^3?). Unworn.
(5) Right upper molar (M^1?). Moderately worn but badly damaged.
(6) Left upper molar (M^1?). Unworn but slightly damaged.
(7) Left upper molar (M^2?). Unworn but slightly damaged. Probably from same individual as B.M. 30346a (6).
(8) Left upper molar (M^3?). Unworn.
(9) Left P^3. Slightly worn.
B.M. M25096. Right P^2. Slightly worn.
B.M. M10267. (1) Left P^2. Unworn.
(2) Right upper canine.

Description. The base of the strong coronoid crest and the shallow masseteric fossa are preserved in B.M. M10260. A small mandibular foramen occurs just below alveolar level. The posterior mental foramen lies between P_3 and P_4.

The lower incisors and P_1–P_2 are unknown from the Headon Beds. The lower canine is known (B.M. 29741) only by the root. P_3, preserved only in B.M. M10260, is oval and double-rooted, with an almost continuous cingulum; it has a main crested cusp which falls to a small anterior cusp and a single-cusped postero-internal talonid. P_4 (unworn in B.M. M10269) is moderately molarised with the protoconid larger than the metaconid. The metaconid is median and posterior to the protoconid. A slight swelling on the postero-internal wall of the metaconid (distinct in B.M. M10269 but indistinct in B.M. M10260) indicates a rudimentary metastylid. These cusps, which are crested transversely, form the oblique posterior trigonid wall. There are small external and antero-external cingula. A straight crest from the protoconid falls antero-basally to a small median paraconid which merges into a prominent antero-internal cingulum. From the prominent hypoconid, a crest runs antero-internally (crista obliqua) to meet the posterior protoconid wall, and internally to join a small but distinct entoconid (posterior to the hypoconid). A low crest from the entoconid runs anteriorly to the base of the metaconid. In B.M. M10260, the P_4 entoconid is vestigial.

In M_1, protoconid and metaconid are subequal when unworn. A metastylid is well differentiated, although it is indistinct in B.M. M10260; this cusp, with the crested paraconid and metaconid forms the strongly oblique posterior trigonid wall. From the protoconid a crest curves antero-internally to meet the paraconid external to the midline. This latter cusp, as in P_4, merges with a strong antero-internal cingulum. There are faint antero-external, external and postero-external cingula. The hypoconid is slightly larger than the more posteriorly situated entoconid; these cusps are joined by crests to a small but distinct median hypoconulid which is slightly posterior to the entoconid. There is a prominent crista obliqua. M_2 is closely similar to M_1, except for its larger size. The trigonid of M_3 is almost identical with that of M_1 and M_2, except for a generally poorly developed metastylid (in B.M. 30323 and B.M. 30856, for example). The hypoconid is strongly developed (as in M_1–M_2), with a prominent crista obliqua. The entoconid is vestigial (B.M. 30856) or represented by a low swelling (B.M. 30323) posterior to the hypoconid. The median hypoconulid (external to the midline in S.M. C53483) is as large as the hypoconid and surmounts a large rounded posteriorly projecting hypoconulid lobe which greatly extends the length of the talonid. From the hypoconulid, a low crest curves antero-internally, forming the internal talonid margin. The hypoconulid lobe is well separated from the hypoconid.

The upper canine alveolus (B.M. M3572) indicates a fairly large curved tooth. An isolated canine (B.M. M10267 (2)) has an almost continuous cingulum, more prominent internally. The tooth is grooved vertically on the anterior and posterior faces. P^1 is known from the Headon Beds only by an alveolus (B.M. M3572) indicating a very small single-rooted externally placed tooth. P^2 is oval and obliquely set in the tooth row (B.M. 25096) with an almost continuous cingulum which is strong generally except antero-externally. There is a large external anteriorly-crested cusp, and a small internal rounded lobe which is variably basined. P^3 is larger than P^2, with a large antero-external cusp and a smaller antero-internal cusp. The tooth is set obliquely in the jaw as in P^2. The antero-external cusp is crested anteriorly and posteriorly. There is a distinct parastyle which is connected to the protocone by a sharp crest. A cingulum is absent round the protocone but elsewhere it is prominent (although very reduced in B.M. 30346a (9)). P^4 is smaller than M^1 but larger and more quadrate than P^3, and set more squarely in the tooth row. The paracone is slightly larger than the metacone; these cusps are sharply crested anteriorly and posteriorly. The protocone and metacone are subequal. As in P^3, a sharp crest runs from the protocone to a distinct parastyle. The cingulum is generally well developed but absent anteriorly.

M^1 is roughly quadrate in outline and larger than P^4. Externally and anteriorly, the tooth is almost identical with P^4, except for a small paraconule midway along the protocone-parastyle crest and a stronger cingulum round the protocone base. There is a hypocone sited slightly internal to the protocone and opposite the metacone; this cusp, the smallest of the major cusps, is joined to the posterior cingulum by a low curved crest. M^2 is larger than M^1, but otherwise structurally nearly identical. M^3 is similar but slightly narrower antero-posteriorly than M^2. The M^3 internal

TABLE 13

Selected measurements (in mm) of *Adapis magnus*

	P_3		P_4		M_1		M_2		M_3	
	a-p	trs	a-p	trs	a-p	trs	a-p	trs	a-p	trs
B.M. 30323	—	—	—	—	6·8	5·1	7·4	5·4	9·3	5·0
B.M. 30856	—	—	—	—	—	—	7·6	5·4	9·4	4·7
B.M. 29864	—	—	6·4	4·8	7·1	5·1	—	—	—	—
B.M. M10260	6·3	4·0	7·1	4·4	7·0	4·8	7·6	5·3	—	—
B.M. M10269	—	—	6·8	4·8	6·9	5·7	7·2	6·1	—	—
B.M. M10267 (3)	—	—	—	—	6·7	5·0	7·3	5·4	—	—
D.M.S.W. M556 (41)	—	—	7·2	5·6	7·2	5·0	8·0	5·6	—	—
B.M. M26057 (1)	—	—	—	—	—	—	7·6	5·3	—	—
B.M. M26057 (2)	—	—	—	—	7·1	4·6	—	—	—	—
B.M. M25093	—	—	—	—	—	—	—	—	8·7	4·2
S.M. C54221	—	—	—	—	—	—	8·1	5·7	—	—
S.M. C53483	—	—	—	—	—	—	—	—	10·2	5·2
S.M. C53477	—	—	—	—	—	—	—	—	9·2	5·1

	P^3		P^4		M^1		M^2		M^3	
	a-p	trs	a-p	trs	a-p	trs	a-p	trs	a-p	trs
B.M. 3572	4·7	5·8	—	—	6·7	7·4	7·0	8·8	7·0	8·8
B.M. M10261 (1)	—	—	—	—	—	—	6·9	8·3	—	—
B.M. M10261 (2)	—	—	—	—	—	—	7·0	8·3	—	—
B.M. M20560 (1)	—	—	—	—	—	—	7·5	8·3	—	—
B.M. M20560 (2)	—	—	6·2	7·5	—	—	—	—	—	—
B.M. M12564 (1)	—	—	—	—	—	—	6·3	8·1	—	—
B.M. M12564 (2)	—	—	6·1	7·2	—	—	—	—	—	—
S.M. C30678	—	—	6·4	7·5	—	—	—	—	—	—
S.M. C30674	—	—	—	—	7·5	9·7	—	—	—	—
S.M. C30679	—	—	—	—	6·9	8·3	—	—	—	—
S.M. C30681	—	—	—	—	—	—	—	—	7·0	8·8
S.M. C53479	—	—	—	—	—	—	—	—	7·0	7·5
S.M. C30662	—	—	—	—	6·6	7·6	—	—	—	—

cingulum in B.M. 30346a (2), is very rudimentary. In some specimens, the antero-internal molar cingulum is continuous with a crest from the hypocone; in other specimens this is not so. This feature is also variable in M^1–M^3 of the same individual, as in B.M. 3572.

REMARKS. The species has long been recognised from the Lower Headon Beds of Hordle Cliff. *Adapis magnus* (*sensu lato*) is subject to considerable variation and several distinct varieties have been recognised (Stehlin, 1912).

The species is distinguished from other species as follows: *A. sciureus* has shorter rounded molars; the protoconid-metaconid crest is only slightly oblique and there is no metastylid; P_3 is more simple and P_4 less molarised with a smaller talonid; the upper molars have a strong metaconule and protoconule and a stronger hypocone. *A. priscus* possesses rounded less elongated molars; the protoconid-metaconid crest is only slightly oblique and there is no metastylid. In *A. ruetimeyeri* the rounded molars lack a metastylid; the protoconid-metaconid crest is only slightly oblique and there is a strong hypocone. *A. parisiensis* is much smaller with the lower molars relatively more elongated antero-posteriorly; the upper molars are less extended transversely; P^3 is extended antero-posteriorly with a smaller internal cingulum and talonid, and the upper canine is smaller and lacks grooves.

Adapis parisiensis (Blainville, 1841)

(Pl. 2, figs 2, 3)

DIAGNOSIS. One third smaller than *A. magnus*, with molars relatively more elongated; metastylid variably developed. Upper canine small, generally lacking a grooved crown; P^3 elongated antero-posteriorly with small talonid and internal cingulum.

HOLOTYPE. A skull, according to Hill (1953), now in the Paris Museum. Late Eocene (Late Ludian); France. Described and figured, Blainville, 1841, p. 112, pl. 9 (Genus *Anoplotherium*).

MATERIAL. F.C.S. 7.

(1) Fragment of left mandibular ramus with M_1–M_3. M_3 is damaged.

(2) Fragment of right mandibular ramus with P_2–M_1, M_3, and alveoli of the canine, P_1 and M_2. Part of the symphysis is preserved.

(3) Right M_2–talonid only.

(4) Left P^2 (?).

(5) Left P^4 with roots embedded in a maxillary fragment.

(6) Left M^1 (?)—internal fragment with protocone only. All specimens from the same individual. Teeth moderately worn. Upper Headon Beds (Lignite Bed), Headon Hill.

DESCRIPTION. The mandible is fairly long. The posterior mental foramen lies below the posterior root of P_4; the larger anterior foramen is sited between the canine and P_1. A small intermediate foramen lies below the anterior root of P_2. The symphysis is long and oblique.

The canine alveolus indicates a semiprocumbent tooth. P_1 (from the alveolus) was small and single-rooted. P_2 is an oval double-rooted tooth with a large anteriorly crested cusp and a small postero-internally projecting talonid. The talonid bears a strong antero-posterior crest which posteriorly is raised into a small cusp. There is a fairly strong internal cingulum and a weak postero-external cingulum. P_3 is double-rooted and similar to P_2, except for a longer talonid and a larger talonid cusp. In P_4, the protoconid and metaconid appear to be subequal but this is obscured by wear on the one specimen. The metaconid is markedly posterior to the protoconid, with a distinct postero-internal metastylid. A straight anterior protoconid crest joins a distinct median paraconid. There is a strong antero-internal shelf-like cingulum and a smaller continuous antero-external, and postero-external cingulum. The hypoconid is joined to the smaller more posteriorly sited entoconid by a curved posterior crest, and joined to the posterior trigonid wall by a strong crista obliqua.

M_1 is almost identical with P_4, except that the entoconid and hypoconid are subequal, and there is a small median hypoconulid slightly posterior to the entoconid. M_2 differs from M_1 only by its larger size. M_3 is very similar but broader and more elongated antero-posteriorly than the other molars; the metastylid is very well developed, being higher when unworn, than the protoconid. The talonid is almost the same as in *A. magnus:* the moderately developed hypoconid is joined to the posterior trigonid wall by an oblique crest; the smaller entoconid is slightly posterior to the hypoconid; the hypoconulid, the largest talonid cusp is extended posteriorly as a prominent rounded median separated lobe.

P^1 is ovoid with a large external cusp which is crested anteriorly and posteriorly; internally the tooth is basined. There is a strong cingulum except externally where it is vestigial. P^4 is slightly elongated transversely. Of the major cusps, the protocone appears to be the largest and the metacone smallest, with the paracone intermediate in size. The paracone and metacone are crested anteriorly and posteriorly. A strong broad crest runs from the protocone to a distinct parastyle. A strong external and posterior cingulum is present. Antero-internally there is a short cingulum; this does not extend round the protocone base. Postero-internally there is little sign of a hypocone differentiated from the cingulum. The M^1 internal fragment shows a strong cingulum which is continuous round the protocone base and a small distinct hypocone.

REMARKS. Distinguished from other species as follows: *A. sciureus* has rounded shorter lower molars; the protoconid-metaconid crest is only slightly oblique and there is no metastylid; P_3 is more simple; P_4 is less molarised with a smaller talonid, and the upper molars have a strong metaconule and protoconule, with a stronger hypocone. *A. priscus* possesses rounded less elongated lower molars; the protoconid-metaconid crest is slightly oblique and there is no metastylid. In *A. ruetimeyeri*, the rounded lower molars lack a metastylid; the protoconid-metaconid crest is slightly oblique and the upper molar hypocone is strong. The presence of P_1, the strongly oblique protoconid-metaconid crest and a prominent metastylid, support reference of this specimen to *A. magnus* or *A. parisiensis.* However, *A. magnus* is much larger and has relatively less elongated lower molars and a slightly more transverse protoconid-metaconid crest.

There is considerable variation in the skull, posterior region of the mandible and molars of *A. parisiensis*. Filhol (1883) recognised six varieties which were reduced to three by Stehlin (1912 : 1235). F.C.S. 7 does not agree closely with any of Stehlin's figured specimens, differing in the greater development of the metastylid and in mandible shape. The material is perhaps best considered as a variety of *A. parisiensis;* it is undoubtedly specifically distinct from *A. magnus* from the Lower Headon Beds.

TABLE 14

Measurements (in mm) of *Adapis parisiensis*

	P_2		P_3		P_4		M_1		M_2		M_3	
	a-p	trs	a-p	trs	a-p	trs	a-p	trs	a-p	trs	a-p	trs
F.C.S. 7 (1)	—	—	—	—	—	—	6·1	4·1	6·6	4·5	8·7	4·0
F.C.S. 7 (2)	4·7	3·0	5·0	3·2	5·6	4·0	5·9	4·2	—	—	8·6	4·8

Family **TARSIIDAE** Gray, 1825

DIAGNOSIS. Zygomatic arches slender. Brain case much expanded transversely. Bullae much inflated; ectotympanic tubular, extends out of bulla. Foramen magnum directed largely downwards. Very short narrow muzzle; palate narrow anteriorly. Tooth rows converge (V-shaped). Upper canine smaller than anterior incisor. Lower canine larger than upper. Hypocone often small. (after Simons, 1961).

REMARKS. Following Simons (1961), the group is divided into two subfamilies:

Tarsiinae Gray, 1825. Recent; East Indies–Philippines.

Microchoerinae Lydekker, 1887. Middle-Late Eocene; Europe.

On the basis of relationship with *Tarsius*, Simons (1961 : 53) placed the Microchoerinae (previously grouped with the Anaptomorphidae) in the Tarsiidae. Following McKenna (1967) and Russell, Louis & Savage (1967), Microchoerinae Lydekker, 1887 is adopted in preference to the previously more widely used Necrolemurinae Simpson, 1940.

Subfamily **MICROCHOERINAE** Lydekker, 1887

DIAGNOSIS. Skull with comparatively large anteriorly-directed orbits. Snout reduced in size with anterior convergence of the tooth rows. Typically the dental formula is $\frac{2}{0}, \frac{1}{1}, \frac{3}{4}, \frac{3}{3}$, with total loss of lower incisors except in one species. Lower canine enlarged and P_1 small and vestigial. Upper canine small and premolariform, the upper enlarged tooth being the most anterior incisor, here considered as I^2. P_4 not elevated, having a short heel and tending towards a molariform condition.

P_2–P_4 low and oval in shape. In M_2–M_3, paraconid fusing with metaconid, the talonid basined and subovate. Upper molars quadrate with large hypocone usually developed on border of a postero-internal basin. Metaconule and protoconule developed and in more advanced forms, numerous accessory cuspules. (compiled from Simpson, 1940, and Simons, 1961).

Remarks. Distinguished from the other subfamily as follows: The Tarsiinae has upper molars with a primitive tritubercular crown, a rudimentary hypocone and a reduced metaconule.

Five genera are currently referred to the Microchoerinae:

Microchoerus Wood, 1884. Late Eocene; Britain, France, Switzerland, Spain.
Necrolemur Filhol, 1873. Middle-Upper Eocene; France, Germany.
Nannopithex Stehlin, 1916. Middle Eocene; Switzerland.
Pseudoloris Stehlin, 1916. Late Eocene; France, Spain.
Agerina Crusafont, 1967. Middle Eocene; Spain.

Microchoerus and *Necrolemur* have long been placed in this subfamily. Recent work by Hürzeler (1948) and Simons (1961 : 61) has added *Nannopithex*, previously only tentatively assigned to the group. Simons has also shown (1961 : 54) that *Pseudoloris*, formerly placed by Simpson (1940 : 198) in the Anaptomorphidae as the single member of a separate subfamily, is closely related to the three former genera and should be placed, therefore, in the Microchoerinae. The genus *Periconodon* from the Middle Eocene of Switzerland, was tentatively assigned to the group by Hill (1955 : 290), but Simons (1962 : 30) referred it to the Omomyidae; more recently, this genus has been placed tentatively in the Adapidae by Russell, Louis & Savage (1967). Crusafont (1967) departed from the generally accepted classification by referring *Pseudoloris* to the Omomyidae.

Genus ***MICROCHOERUS*** Wood, 1844

Diagnosis. Upper molars with hypocone, mesostyle and numerous accessory cuspules; M_3 with a prominent wide rounded posterior lobe, separated from hypoconid and entoconid by small constrictions; small though distinct paraconid on M_1, not distinct on M_2 and M_3. Extensive enamel crenulations on lower molars.

Type species. *Microchoerus erinaceus* Wood, 1844. Lower Headon Beds (Mammal/Crocodile Bed), Hordle Cliff.

Remarks. Distinguished from other genera as follows: *Pseudoloris* is much smaller with sharp cusps; the molars lack enamel crenulation and accessory cuspules; upper molars lack a mesostyle; the lower molars have a distinct paraconid and the M_3 hypoconulid lobe is narrow, sharp and well separated. *Nannopithex* is smaller with only slight enamel crenulation; no mesostyle is developed and the M_3 hypoconulid lobe is narrower and more distinctly separated. *Necrolemur* has only slight enamel crenulation in the molars and lacks a mesostyle, and the M_3 hypoconulid lobe is less developed.

Three species have been described:

M. erinaceus Wood, 1844, p. 350. Late Eocene (Early Ludian); Britain, France, Spain.

M. edwardsi (Filhol, 1880), p. 124. Late Eocene (Late Ludian); Britain, France.

M. ornatus Stehlin, 1916, p. 1377, pl. 22, fig. 12. Late Eocene (Late Ludian); Switzerland, Spain.

M. erinaceus and *M. edwardsi* are known from parts of the maxillae and fragmentary mandibles; *M. ornatus* is based on a partial upper dentition.

Crusafont (1967) considered that *Microchoerus edwardsi* was synonymous with *M. erinaceus*. In the same work, Crusafont (1967) referred *Microchoerus erinaceus* to *Necrolemur* and considered *Necrolemur antiquus* Filhol as a synonym of '*Necrolemur*' *erinaceus; Microchoerus* (*sensu stricto*) was retained for the species *M. ornatus*.

Microchoerus erinaceus Wood, 1844

(Pl. 3; Pl. 4)

DIAGNOSIS. Dental formula $\frac{2}{0}, \frac{1}{1}, \frac{3}{4}, \frac{3}{3}$. The largest species. Apparently lacks lower incisors. Upper molars only moderately complex, lacking duplicated paraconule. P^3 with rounded outline and a single large external cusp.

HOLOTYPE. B.M. 25229 (1). Fragment of left mandibular ramus with P_4–M_3. (2) Palatal fragments with an almost complete dentition, lacking only the left canine and right I^2 (latter tooth reconstructed in plaster). Fairly badly worn. Lower Headon Beds (Mammal/Crocodile Bed), Hordle Cliff. Listed and described, Wood, 1844 : 350; Figured, Wood, 1846 : 12, figs 1 and 3; Described and figured, Lydekker, 1885d : 529, fig. (unnumbered); Figured (upper), Lydekker, 1887 : 304, fig. 45; Described and figured, Cooper, 1910 : 40, pl. 3, fig. 1; Described and figured, Simons, 1961 : 59, fig. 2.

MATERIAL. All specimens from the Lower Headon Beds (Mammal/Crocodile Bed), Hordle Cliff, except where stated otherwise.

B.M. 10768. Fragment of right mandibular ramus with M_1–M_3. Fairly badly worn; crowns damaged.

B.M. M12563 (1). Fragment of left mandibular ramus with P_4–M_2.
(2). Fragment of right mandibular ramus with M_1–M_3.
(3). Isolated M_3, probably from (1) above.

B.M. 30346. Fragment of left mandibular ramus with M_1–M_2.

B.M. 30346b (1). Fragment of left mandibular ramus with M_2 and broken M_1.
(2). Fragment of right mandibular ramus with M_3.
(3). Fragment of left mandibular ramus with P_4–M_3.
(4). Fragment of right maxilla with M^1–M^3.
(5). Right M^2.
(6). Right P^4.

Mentioned by Lydekker, 1887, p. 304. (4) above, listed Cooper, 1910 : 40.

B.M. M2605b. Isolated M_1, M_2 and M_3, from same individual.

S.M. C9672. Left mandibular ramus with M_1–M_3. Posterior region almost complete. Listed and figured, Cooper, 1910 : 39; pl. 3, fig. 6.

S.M. C9681. Left mandibular ramus with P_3–M_3 and the alveoli of the canine, P_1 and P_2. The symphysis is preserved.

S.M. C9670. Left mandibular ramus with P_2–M_3. Listed and figured, Cooper, 1910 : 40; pl. 3, fig. 4.

S.M. C9671. Right mandibular ramus with P_3–M_3 and roots of the canine, P_1 and P_2. Symphysis preserved. Listed, Cooper, 1910 : 39. According to Cooper, associated with S.M. C9670.

S.M. C9673. Fragmentary right mandibular ramus with M_1–M_2, damaged M_3 and roots of P_4. Listed, Cooper, 1910 : 40.

S.M. C9675. Fragmentary right mandibular ramus with P_4–M_2.

S.M. C9678. Right M_3.

S.M. C9679. Right M_2. Probably from same individual as S.M. C9678.

S.M. C9680. Fragment of right mandibular ramus with P_4 and M_1. Probably from same individual as S.M. C9678.

S.M. C54174 (1). Right P_3. Unworn, slightly damaged.
(2). Left M_1. Talonid only. Almost unworn. Lower Headon Beds (Rodent Bed), Hordle Cliff.

S.M. C53482. Fragment of left mandibular ramus with roots of P_4, M_1, and alveoli of the canine and P_1–P_3.

B.M. M26055. Fragment of left mandibular ramus with P_2–M_3. P_3 damaged. Teeth badly worn. Upper Headon Beds (*Microchoerus* Bed), Headon Hill.

F.C.S. 3. Left M_3. Upper Headon Beds (Lignite Bed), Headon Hill.

B.M. M12563 (1). Right M^2.
(2). Left M^1.

S.M. C9669. Palatal fragment with right and left M^2–M^3. Listed, Cooper, 1910, p. 39.

S.M. C30710–27. Teeth mounted on a board:
  S.M. C30712. Left M^2.
  S.M. C30714. Left M^2.
  S.M. C30715. Left M^1.
  S.M. C30716. Right M_1.
  S.M. C30717. Right M_2.
  S.M C30718. Left M^1.
  S.M. C30719. Right P^4.
  S.M. C30720. Left P^4.
  S.M. C30723. Left M_1.
  S.M. C30724. Right M_2.
  S.M. C30727. Right upper canine.

B.M M12565a (1). Right M_1.
(2). Right M_1 (or M_2).
(3). Right M^1.

(4). Right I^2 (?).
(5). Right upper canine (?).
B.M. M12565c (1). Left upper canine (?).
(2). Right P^3. Partially embedded in matrix.
B.M. M25090 (1). Left I^2 (?).
(2). Left I^3 (?). Both moderately worn.
S.M. C54175 (1). Left P^3. Moderately worn.
(2). Left upper canine (?). Lower Headon Beds (Rodent Bed), Hordle Cliff.

Description. The mandible is fairly short and stout; the oval-shaped symphysis (S.M. C9681, S.M. C9671, and S.M. C9670) is steeply inclined, following the line of the canine root. Below P_3, the lower edge of the mandible projects internally as a small shelf. The smaller posterior mental foramen lies below P_4 (S.M. C9671) and S.M. C9681), or slightly anterior to this (S.M. C9670 and S.M. C53482). The position of the larger anterior mental foramen varies from below P_3 (S.M. C9671 and S.M. C9681) to below P_2 (S.M. C9670). The posterior region is preserved only in S.M. C9672 (wax restoration of the type excepted). The moderately developed rounded angular process falls considerably below the lower anterior margin of the mandible. The mandibular foramen lies just below alveolar level. The coronoid is small, the posterior margin rather damaged on the specimen. The slender condyle has an articulating surface which is slightly elongated transversely; it lies considerably above the tooth row level. The coronoid crest is more prominent than the condyloid crest, although both are not well developed.

The tooth row is compact and continuous. In M_3 the protoconid and metaconid are subequal and larger than the hypoconid and entoconid. A small crest which unites the protoconid and metaconid follows the rounded anterior tooth margin; there is no distinct cuspate paraconid. A crest from the hypoconid runs antero-internally towards the metaconid. The posterior region of the talonid is separated into a prominent rounded hypoconulid lobe which is slightly displaced internally; this lobe greatly increases the length of the talonid. In B.M. 10768, the hypoconulid lobe is considerably enlarged relative to the other specimens. There is no distinct cuspate hypoconulid but the lobe bears an internal and an external accessory cusp; these accessory cusps are rather indistinct in some specimens especially after wear. There is a fairly strong external cingulum (only weakly developed in S.M. C9672). Several specimens show slight traces of an internal cingulum.

M_2 is more quadrate than M_3 but otherwise very similar without the hypoconulid lobe. No paraconid is distinguishable as in M_3; the protoconid, metaconid and hypoconid are subequal in size, the entoconid smaller. There is a small bilobed median hypoconulid on the hypoconid-entoconid crest (indistinct on S.M. C9681). In most specimens, there is an accessory cuspule (mesoconid) on the prominent crista obliqua. A strong external cingulum is present (weak in S.M. C9672) but there is no trace of an internal cingulum.

M_1 is similar structurally to M_2, with a small duplicated hypoconulid on most specimens (not distinguishable on S.M. C9671) and a mesoconid. There is no internal cingulum. The tooth differs from M_2 and M_3 by having a more squared anterior margin and a small distinct paraconid situated directly anterior to the metaconid; the paraconid is separated from the metaconid but united to the protoconid by a low crest.

P_4 is smaller and subtriangular with a small low heel. The tooth is dominated by a large median protoconid. A curved antero-basally directed crest from the protoconid forms the anterior tooth margin; the posterior face of the protoconid bears two crests. The smaller separated metaconid in S.M. C9680, S.M. C9670, S.M. C9671 and S.M. C9675 is more posteriorly placed than the protoconid and falls to a strong antero-internal cingulum. In the holotype (B.M. 25229) and S.M. C9681, the protoconid and metaconid are opposite and the internal cingulum is only weakly developed. S.M. C9681 and S.M. C9670 have a well developed external cingulum; this is poorly developed in S.M. C9680, S.M. C9674 and S.M. C9681.

P_3 (well preserved in S.M. C9681, S.M. C9671 and S.M. C9670) bears a large median anteriorly crested cusp and a small cingulum-like heel; there is a strong internal cingulum. In S.M. C9671 and S.M. C9670 the anterior crest runs parallel to the length of the tooth; the main cusp slopes moderately basally towards the heel, bounded by two sharp crests; an external cingulum is moderately developed. In S.M. C9681, the anterior crest curves round towards the internal cingulum; the main cusp is more posteriorly situated, falling more steeply to the heel and the two posterior crests are less prominent.

P_2 (S.M. C9670 and B.M. M26055) is made up of an anteriorly-crested cusp and a small cingulum-like heel. The cusp is concave internally and convex externally. There is a prominent internal cingulum and a smaller external cingulum.

P_1, represented only by an alveolus (S.M. C9681) and a broken root (S.M. C9671) was evidently a small anteriorly inclined tooth, situated on the external edge of the tooth row. The broken root (S.M. C9671) and a large oval deep alveolus (S.M. C9681) of the lower canine indicate a large anteriorly-inclined tooth, lying at a much lower level in the jaw than the other teeth.

I^2–P^4 are associated only in the holotype. The most anterior tooth I^2, is enlarged with almost vertical sides. I^3 is considerably smaller with an antero-internally sloping crown and a small external cingulum. The semi-procumbent canine is much enlarged (but not as high as I^2) and has an external cingulum. P^2 is single-rooted and semi-procumbent with a small heel; the tooth is smaller than the canine.

P^3 and P^4 are quadrate and larger than P^2; both have a single large external cusp and a strong external cingulum. P^4 has a small antero-internal and a small postero-internal cusp which are sharp and unworn in S.M. C30719 and S.M. C30720; these are worn down to an antero-posterior ridge in the holotype and B.M. 30346b (6).

M^1 and M^2 are quadrate and subequal in size; the metacone lies on a straight antero-posterior line with the paracone. In the smaller M^3, with a more rounded posterior margin, the metacone is more internal to the paracone. The hypocone, which in M^1 is almost equal to the protocone, becomes progressively smaller in M^2 and M^3. A paraconule and metaconule are well developed in all molars, the former sited anterior of a line between protocone and paracone, the latter anterior of a line between metacone and hypocone. The metaconule, equal to the paraconule in M^1, becomes progressively smaller in M^2 and M^3. In all molars, a small accessory cusp is situated midway between the metaconule and the protocone; this can be regarded as a duplication of the metaconule. In M^1 and M^2, this accessory cusp is smaller than the main metaconule, but in M^3 it is larger. There is a prominent mesostyle in M^1 and M^2 external to a line between the paracone and metacone. This cusp is represented in M^3 by a slight cingular swelling. A small but definite hypostyle occurs on M^1 and M^2 of B.M. 30346b (4). A parastyle and metastyle are encountered more frequently, appearing as upgrowths from the prominent external cingulum: a parastyle occurs on M^2 of S.M. C30712 and S.M. C30714 and M^1 of B.M. 30346b (4), B.M. M12563 (2), S.M. C30715 and S.M. C30718; the metastyle is present on M^2 of the holotype (B.M. 25229), B.M. 30346b (4), S.M. C30712 and S.M. C30714 and the M^1 of B.M. 25229 and B.M. 30346b (4). In all other specimens, these three accessory cusps are indistinct.

REMARKS. The number of specimens is really inadequate for any satisfactory statistical treatment of variation within the species to be carried out. However, some tentative conclusions may be drawn from the available material. The following variates were considered: length and width of M_3, M_2, M_1 and P_4; length of tooth rows M_1–M_3 and P_4–M_3 and the internal depth of the mandible below the posterior

TABLE 15

Selected measurements (in mm) of *Microchoerus erinaceus*

	P_2		P_3		P_4		M_1		M_2		M_3		M_1–M_3
	a-p	trs	a-p	trs	a-p	trs	a-p	trs	a-p	trs	a-p	trs	a-p
B.M. 25229 (1)	—	—	—	—	3·0	2·8	4·2	3·6	—	(3·4)	4·3	3·0	11·0
B.M. 10768	—	—	—	—	—	—	(2·5)	(2·9)	3·8	3·2	4·5	2·7	—
B.M. M12563 (1)	—	—	—	—	3·0	2·6	4·1	3·9	4·2	3·9	—	—	—
B.M. M12563 (2)	—	—	—	—	—	—	4·2	3·7	4·3	3·6	4·8	3·2	—
B.M. 30346	—	—	—	—	—	—	4·6	3·4	4·9	3·4	—	—	—
B.M. M26055	3·4	2·1	—	2·4	3·4	2·7	4·3	3·2	4·0	3·0	4·4	2·8	—
S.M. C9670	3·0	2·2	3·1	2·3	3·5	2·8	3·7	3·4	3·7	3·4	4·5	3·0	11·8
S.M. C9671	—	—	3·1	2·3	3·3	2·9	3·8	3·5	3·7	3·4	4·6	3·1	11·9
S.M. C9681	—	—	3·1	2·4	3·4	2·9	4·2	3·5	3·9	3·4	4·2	2·5	12·0
S.M. C9672	—	—	—	—	—	—	4·1	4·0	4·0	3·5	4·6	3·0	12·5
S.M. C9673	—	—	—	—	—	—	4·0	3·2	4·0	3·2	—	—	—
S.M. C9675	—	—	—	—	3·5	3·0	4·3	3·9	4·4	3·7	—	—	—

	P^2		P^3		P^4		M^1		M^2		M^3	
	a-p	trs	a-p	trs	a-p	trs	a-p	trs	a-p	trs	a-p	trs
B.M. 25229 (2)	—	—	2·9	3·5	3·1	3·8	4·0	4·6	3·6	5·0	3·0	3·9
B.M. 25229 (2)	2·9	2·4	2·7	3·5	3·0	4·2	4·0	4·7	3·9	4·9	3·2	4·0
B.M. 30346b (4)	—	—	—	—	—	—	4·2	5·0	4·0	4·9	2·8	4·0
B.M. 30346b (5)	—	—	—	—	—	—	—	—	4·1	4·7	—	—
B.M. 30346b (6)	—	—	—	—	3·4	3·8	—	—	—	—	—	—
B.M. M12563 (1)	—	—	—	—	—	—	—	—	3·9	5·1	—	—
B.M. M12563 (2)	—	—	—	—	—	—	4·2	4·9	—	—	—	—
S.M. C9669	—	—	—	—	—	—	—	—	3·9	(4·8)	3·1	4·2
S.M. C9669	—	—	—	—	—	—	—	—	3·8	5·0	3·0	4·2
S.M. C30715	—	—	—	—	—	—	—	4·4	—	—	—	—
S.M. C30719	—	—	—	—	—	3·8	—	—	—	—	—	—
S.M. C30720	—	—	—	—	—	3·4	—	—	—	—	—	—

margins of M_3, M_1 and P_3. The mandible depth in *M. erinaceus* appears to be highly variable and cannot be correlated with individual age as reflected by dental wear. Frequency distributions utilising dimensions of the posterior lower teeth indicate a separation of the larger specimen B.M. 30346; this is removed by secondary grouping of the data and is, in all probability, due only to incomplete sampling. P^3–P^4 of the type specimen (B.M. 25229 (1)) and S.M. C9681 are different structurally from the rest of the material. These differences might be sexual or could possibly indicate an anterior milk dentition; they are unlikely to be of specific importance.

Simons (1961) observed an alveolus anterior to the lower canine in some French specimens of *M. edwardsi*, indicating at least one lower incisor. There is no evidence for similar teeth in the specimens of *M. erinaceus* from the Headon Beds. But preservation of this region of the mandible is rare and their absence in *M. erinaceus* should be treated with caution. Apart from the probable structural difference in dentition, *M. erinaceus* differs from *M. edwardsi* by its greater size.

Several features of the upper dentition distinguish the species from *M. ornatus* (known only from upper dentition): P^3 in *M. erinaceus* has a rounded outline and a single major external cusp whilst this tooth in *M. ornatus* has a squared outline and two external cusps. In addition to the duplicated metaconule present in both species, the M^2 of *M. ornatus* is further complicated by a duplicated paraconule and a prominent hypostyle. *M. erinaceus* is significantly larger than *M. ornatus*: in the holotype of *M. erinaceus*, the length of the tooth row, M^2–M^3 is 11·0 mm, whereas in the holotype of *M. ornatus*, this measurement is 9·0 mm.

Genus ***PSEUDOLORIS*** Stehlin, 1916

DIAGNOSIS. Small size. No accessory cuspules and enamel crenulations. Upper molars relatively elongated transversely, lacking mesostyles; cingulum-hypocone distinct on M^1 and M^2, indistinct on M^3; lower molar cusps relatively sharp and separated. M_3 entoconid and hypoconulid high and separated with distinct narrow hypoconulid-lobe. Distinct small paraconid on M_1 and M_2, reduced on M_3.

TYPE SPECIES. *Pseudoloris parvulus* (Filhol, 1890). ? Late Eocene (Quercy Phosphorites); France.

REMARKS. The genus was proposed by Stehlin (1916 : 1397) for a species originally described by Filhol, (1890a) as *Necrolemur parvulus*. The validity of this genus has been subsequently accepted generally.

Simpson (1940 : 198) agreeing with Teilhard de Chardin (1916–1921a) that *Pseudoloris* was significantly *Tarsius*-like, erected a new subfamily, Pseudolorisinae, for this monospecific genus. Recently Simons (1961 : 54) has shown that the similarities between *Pseudoloris* and other microchoerines are so great, that separation at subfamily level is not possible.

Weigelt (1933) described *P. abderhaldeni* from the Middle Eocene brown coal deposits of Geiseltal, Germany. Simons (1961 : 61) stated that the type of this species is conspecific with '*Necrolemur*' *raabi* Heller, the latter species being referable to *Nannopithex*. Crusafont (1967) described a new species, *Pseudoloris reguanti* from the Upper Ludian of Spain.

Pseudoloris is distinguished from other genera as follows: *Microchoerus* has a mesostyle and is markedly larger with lower rounded cusps; the M_3 hypoconulid-lobe is wide and rounded and the molars possess numerous accessory cuspules and enamel crenulations. In *Necrolemur* the M_3 hypoconulid-lobe is wide and rounded; the cusps are lower, rounded and less distinct and the genus is much larger. *Nannopithex* has slight enamel crenulations in all teeth; P_4 is much larger than the lower molars; the molar cusps are more rounded and lower, and M_3 entoconid and hypoconulid are not as high and separated.

Pseudoloris parvulus (Filhol, 1890)

(Text-fig. 23)

1890 *Necrolemur parvulus* Filhol.

DIAGNOSIS. As for genus.

HOLOTYPE. Fragment of left mandibular ramus with P_3–M_3 and alveoli of the canine, P_1–P_2. ?Late Eocene (?Ludian, Quercy Phosphorites); Caylux, France. Described and figured, Filhol (1890a : 39, text-fig., unnumbered). Specimen not located by Teilhard de Chardin (1916–1921a : 5). Abundant referred material described and figured by Stehlin (1916 : 1397) and Teilhard de Chardin (1916–1921a : 4).

MATERIAL. B.M. 36812f. Fragment of right mandibular ramus with M_2–M_3. Teeth slightly worn. Lower Headon Beds (Mammal/Crocodile Bed), Hordle Cliff.

DESCRIPTION. M_2 and M_3 are elongated antero-posteriorly. The trigonid and basined talonid are well differentiated, but the cusps are low, the trigonid cusps being only slightly higher than those of the talonid.

In M_2, the trigonid and talonid are subequal in width but the trigonid is compressed antero-posteriorly and is shorter. The protoconid is slightly higher than the metaconid and markedly more anteriorly placed; both cusps are crested transversely. The metaconid is internal in position; the protoconid tip lies just external to the longitudinal midline. There is a well developed antero-external cingulum. A small median cuspate paraconid forms the sharp anterior trigonid apex; this cusp is joined by a small low crest from the metaconid and from the protoconid. The talonid is strongly basined. The entoconid is slightly smaller than the metaconid; a sharp crest runs anteriorly from the entoconid to meet, at the base of the posterior trigonid wall, a sharp metaconid crest. Although the tooth is damaged externally, it appears that the hypoconid was opposite, or just anterior to the entoconid, a strong crista obliqua running from this cusp to the base of the posterior protoconid wall. A rudimentary hypoconulid is represented as a very small projection on the posterior talonid margin, just external to the midline; this is joined to the hypoconid and entoconid by small crests. Owing to damage, the extent posteriorly of the cingulum cannot be observed; it may have been continuous round the base of the hypoconid as in M_3.

The anterior part of M_3 is very similar to that of M_2, differing only in minor features: the protoconid is slightly more externally placed, and is subequal with the metaconid; the posterior trigonid margin is less oblique than in M_2 and the paraconid is slightly less developed and more crestiform in appearance, forming a more rounded anterior trigonid apex. The anterior part of the talonid is also very similar. M_3 differs markedly from M_2 by having a hypoconulid-lobe. This long prominent separated lobe is narrow and mainly median although the posterior extremity is slightly internally directed. The lobe, consisting of a single large crestiform cusp, is connected with the hypoconid and entoconid by crests. A prominent continuous antero-external, external and postero-external cingulum is present.

REMARKS. Recently *Pseudoloris parvulus* has been recorded by Crusafont from the Early Ludian of Sosis, Spain (1965, 1967) and Euzet-les-Bains, France (1967). The single specimen from the Headon Beds appears to agree precisely with additional material of *Pseudoloris parvulus* figured by Stehlin (1916), Teilhard de Chardin (1916–1921a) and Piveteau (1957); it constitutes the first record of the genus from the Early Ludian of Britain.

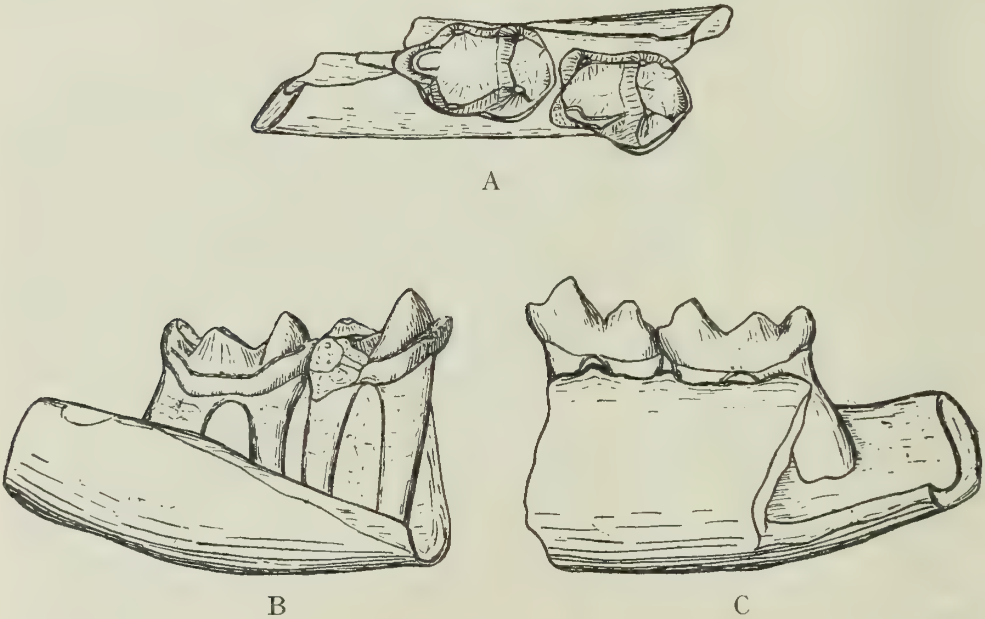

FIG. 23. *Pseudoloris parvulus* (Filhol, 1890). Fragmentary right mandibular ramus with M_2–M_3. B.M. 36812f ×12. Lower Headon Beds, Hordle Cliff. (A) Occlusal view. (B) External view. (C) Internal view.

TABLE 16

Measurements (in mm) of *Pseudoloris parvulus*

	M_2		M_3	
	a-p	trs	a-p	trs
B.M. 36812f	1·6	1·25	1·9	1·2

Order CREODONTA

Family **HYAENODONTIDAE** Leidy, 1869

DIAGNOSIS. $\mathrm{P}\frac{1}{1}$ double-rooted except in some specialized genera; P^3 lacking distinct protocone; $\mathrm{M}\frac{1}{2}$ or $\mathrm{M}\frac{2}{3}$ functioning as main carnassials; $\mathrm{M}\frac{3}{3}$ present or absent; cheek teeth row moderate to long; $\mathrm{M}\frac{3}{3}$ when present transversely extended. Jaw long and shallow to moderately short and deep, with symphysis weak to fairly robust, and angle long, slender, projecting and upcurved at tip. Face long to moderately short; basicranial region narrow to moderately wide; no preglenoid crest (mainly from Denison, 1938 : 117).

REMARKS. The order Creodonta is retained here in a restricted sense, following Romer, (1966 : 229). The family is known from the Early Eocene-Middle Oligocene of North America; Early Eocene-Late Oligocene of Europe; Late Eocene-Oligocene, Early Pliocene of Asia and the Early Oligocene, Early Miocene of Africa.

Denison (1938) distinguished four subfamilies: Proviverrinae, Hyaenodontinae, Limnocyoninae and Machaeroidinae; this was followed by Simpson, (1945). Gazin (1946) proposed a new family, Limnocyonidae, to accommodate the latter two subfamilies. Van Valen (1966) placed all four subfamilies in the Hyaenodontidae but reduced them to the rank of tribes; Gazin's two fold subdivision was retained as two subfamilies, the Hyaenodontinae and the Limnocyoninae. More recently, Van Valen (1967) has abandoned the use of tribes within the Hyaenodontinae, grouping together the Hyaenodontini and the Proviverrini. In the present work, the earlier scheme of Denison is utilized as it provides a simple working arrangement (see also Savage, 1965).

Subfamily **HYAENODONTINAE** Trouessart, 1885

DIAGNOSIS. Long faced, narrow skulled genera; main carnassials $\mathrm{M}\frac{2}{3}$ with carnassial specialization very advanced; M_3 present, M^3 variably present or absent; molars sectorial, length greater than width; M^3, where present, small and transverse; M^1 and M^2 with paracone and metacone completely or nearly connate and protocone reduced or absent; lower molars lack metaconid, talonid vestigial or absent. Body compact, robust; limbs and feet cursorial (after Matthew, 1909 and Savage, 1965).

REMARKS. Distinguished from the other subfamilies as follows: in the Proviverrinae, the metaconid is retained; the carnassial specialization is less advanced and M^3_3 are invariably present. The Limnocyoninae and Machaeroidinae both have M^1_2 functioning as the main carnassials. Savage (1965) listed five good genera in the Hyaenodontinae:

Hyaenodon Laizer & Parieu, 1838. Late Eocene-Late Oligocene; Europe. Late Eocene-Middle Oligocene; North America, Asia. Early Oligocene, Early Miocene; Africa.
Pterodon Blainville, 1839. Late Eocene-Early Oligocene; Europe. Late Eocene-Early Oligocene; North America. Early Oligocene, Early Miocene; Africa. Late Eocene; Asia.
Apterodon Fischer, 1881. Early-Middle Oligocene; Europe. Early Oligocene; Africa.
Metapterodon Stromer, 1926. Early Miocene; Africa. Early Oligocene; Europe.
Leakitherium Savage, 1965. Early Miocene; Africa.

Simpson (1945) listed *Hemipsalodon* Cope, 1885; *Dasyurodon* Andreae, 1887 and *Propterodon* Martin, 1906. Savage (1965) has considered that *Hemipsalodon* is a synonym of *Pterodon* and *Dasyurodon* a synonym of *Apterodon*. More recently, Van Valen (1966 and 1967) has asserted the generic validity of *Hemipsalodon* and has stated (1967) that *Metapterodon* is a synonym of *Pterodon;* he also adds *Ischnognathus* Stovall, 1948 (Van Valen, 1966 and 1967) and (tentatively) *Hyainailouros* Biedermann, 1863 (Van Valen, 1967). *Propterodon* is not well known (see Van Valen, 1966 : 75) and Savage has stated (personal communication) that this latter genus will probably prove to be invalid. According to Van Valen (1967), *Megalopterodon* Dashzeveg, 1964, is synonymous (provisionally) with *Pterodon*. *Apterodon* was referred by Van Valen (1966) to the Mesonychidae; the genus was returned to the Hyaenodontidae by Van Valen (1967) following the work of Szalay (1967).

Genus *HYAENODON* Laizer & Parieu, 1838

DIAGNOSIS. Dental formula $\frac{3}{3}, \frac{1}{1}, \frac{4}{4}, \frac{2}{3}$; M^2 with shallow groove on completely connate paracone and metacone; molars without protocone; metastyle strongly elongated, especially on M^2. Main carnassial pair M^2_3, with M^1_2 as accessory carnassials. M_3 without talonid, M_{1+2} with or without vestigial talonid (Savage, 1965).

TYPE SPECIES. *Hyaenodon leptorhynchus* Laizer & Parieu, 1838. Middle Oligocene (Chattian); France.

REMARKS. Distinguished from other genera as follows: in *Pterodon*, M^3 is present and a small protocone and large parastyle occur on M^1 and M^2. In *Apterodon*, a protocone is present on M^1 and M^2, and M_1 possesses a prominent three-cusped talonid. M^3 is present in *Metapterodon* and M^1 and M^2 possess a strong protocone. *Leakitherium* has a strong protocone on P^4–M^2.

A complete list of species attributed to *Hyaenodon* has been given by Savage (1965). Some 36 species have been described: 9 are from North America, 3 from Asia, 20 from Europe and 4 from Africa, the latter being grouped by Savage as a distinct subgenus. Specific distinctions are based considerably on size differences. Numerous structural features have also been utilized (listed in Savage, 1965), but have nearly all proved highly variable. Many of the early European types are lost and the existing figures and descriptions are frequently quite inadequate. Of the described species, many are undoubted synonyms; several true genera probably are involved. In the absence of a greatly needed thorough revision of the genus, some attempt is made below to clarify the systematics of the Headon Beds specimens.

Hyaenodon c.f. ***minor*** Gervais, 1848–52

(Pl. 5)

1926 *Hyaenodon aimi* Cooper: 370, fig. B.

DIAGNOSIS. M_3 with talonid trace usually present but variably developed. M_1–M_2 usually with distinct cuspule at base of antero-internal paraconid face. P_1 with a single root.

HOLOTYPE. Right mandibular ramus with P_2–M_3 and alveoli of the canine and P_1. Molars badly worn. Late Eocene (Early Ludian); France. Described and figured, Gervais, 1848–52 : 129; pl. 25, fig. 9. Specimen not located.

MATERIAL. All specimens from Lower Headon Beds (Mammal/Crocodile Bed), Hordle Cliff, except where stated otherwise.

B.M. 29752. Complete mandible attached at symphysis. With right canine, P_2–M_3, broken root of P_1 and alveolus of I_3; and left P_2–M_3, broken root of canine and alveolus of P_1. Teeth very badly worn—often to root level. The posterior region of both rami is complete. Labelled in British Museum (N.H.) as '*Hyaenodon hantonensis*'. Listed by Lydekker, 1884 : 444, 1885a : 25.

S.M. C31347 a-c, d, k. Probably all from same individual. Fine greenish-white sand matrix. Teeth well worn.

a. Right mandibular ramus with canine, P_4–M_3, and alveoli of P_1–P_3. M_1 is badly damaged. Posterior region preserved. Figured, Cooper, 1926 : 372, fig. A.

b. Left mandibular ramus with canine, P_2, P_4–M_3. P_3 represented by broken roots.

c. Fragment of right maxilla with P^4, damaged fragment of M^1, alveoli of P^3 and M^2. Anterior part of the zygomatic arch preserved.

d. Fragment of left maxilla with P^4–M^2 and roots of P^3.

k. Isolated left upper canine. Tip damaged.

S.M. C31344. Fragment of left mandibular ramus with P_4–M_2. Moderately worn.

B.M. 29814. Left M_3. Badly worn. Listed by Lydekker, 1885a : 26. (erroneously as right M_3).

S.M. C31346. Left P_3. Moderately worn.

S.M. C30775. Fragment of left maxilla with I^3, P^3–P^4, alveoli of the canine, M^1–M^2 and roots of P^1 and P^2. Teeth damaged. Internal surface embedded in fine greenish sand matrix.

B.M. M25073. Fragment of left maxilla with P^1–P^3, posterior alveoli of P^4 and part of the canine alveolus.

B.M. M25074. Fragment of right mandibular ramus with P_3–M_3. Moderately worn.

B.M. M13075. Fragmentary right and left mandibular rami, not attached at symphysis. Same individual. Adhering matrix of shelly orange sand. Holotype of '*Hyaenodon aimi*'. Described and figured Cooper, 1926 : 370, fig. B.

Right ramus with I_3 and the canine, P_2–M_3 and alveoli of I_2 and P_1. Tip of canine missing.

Left ramus with the canine, P_2–M_3 and alveolus of P_1. Tip of canine missing.

B.M. M25075. Fragment of left maxilla with P^2–M^2. Unworn. Upper Headon Beds (Lignite Bed), Headon Hill.

Description. The mandible is moderately elongated. The posterior mental foramen lies under the posterior root of P_3, the anterior mental foramen at a higher level, under the root of P_1. The symphysial surface is inclined at 45° to the tooth row and ends posteriorly under P_3. The posterior mandibular region is well preserved in B.M. 29752. The prominent transversely elongated condyle, situated below the level of the tooth row, is separated from a small narrow angular process by a strong notch. The angular projects downwards just below the level of the anterior mandibular margin. The coronoid is moderately well-developed with a slightly notched posterior margin. The mandibular foramen is sited markedly posteriorly, just below condyle level. The coronoid and condyloid crests are prominent.

I_2 is represented in the holotype of '*Hyaenodon aimi*' (B.M. M13075) by a small alveolus. I_3 is a small semiprocumbent tooth immediately external to the I_2 alveolus and pressed up close against the canine. I_1 may have been present but no evidence remains. Cooper (1926 : 371) stated that the incisors were not preserved.

The lower canine is large and sharp with an ovoid section. In the right ramus of S.M. C31347, this tooth is probably somewhat displaced from its alveolus. P_1 is represented by the alveolus; this single-rooted tooth was slightly separated from the canine. In S.M. C31347b, the left ramus anomalously lacks a P_1 alveolus and there is a larger gap between P_2 and the canine. Contrary to the statement by Cooper (1926 : 371, footnote) P_1 was originally present in the right ramus of B.M. 29752, as a root-filled alveolus is visible. P_2 is double-rooted, posteriorly-directed and immediately posterior to P_1; it bears a large central cusp which is postero-externally crested. There is usually a continuous internal and postero-internal cingulum, but in B.M. M13075, it is small and antero-internal in position. P_3 is similar to P_2 except that the tooth is longer antero-posteriorly and has a small posterior longitudinally crested cusp; there is no distinct posterior cingulum in B.M. M13075. P_4 is similar to P_3 but larger transversely and strongly inclined posteriorly. The cingulum is usually prominent antero-internally and postero-internally, although indistinct in B.M. M13075. Where the anterior crest of the main cusp merges with the antero-internal cingulum there is an irregular cuspule (S.M. C31347 and B.M. M25074) or a distinct cusp (S.M. C31344, B.M. M13075 and B.M. 29752).

M_1 is very small. The protoconid is slightly larger than the paraconid when unworn; these crestiform cusps are separated by a cleft. A small low talonid bears an elongated cusp. The antero-internal paraconid face (S.M. C31344) bears a small projecting cuspule which is closely pressed against the postero-internal margin of P_4; this cuspule is indistinct in B.M. M13075. On the antero-external paraconid face there is a vertical buttress pressed up against the postero-external margin of P_4. The cingulum is vestigial. In B.M. 29752, only worn rounded stumps of this tooth remain.

M_2 is similar to M_1 but of larger size. The crested paraconid and protoconid, well separated by a cleft, form good shearing facets. The antero-internal cuspule and antero-external buttress are usually well developed; the cuspule is higher than in M_1 and is not in contact with the adjacent anterior tooth. The cuspule is indistinct in B.M. M13075. The posterior talonid cusp is prominent. In B.M. 25074, this tooth is structurally similar but very small, being about the same length as M_1.

M_3 is markedly elongated in length; the crested paraconid is separated from the larger protoconid by a deep cleft; these cusps together form an effective slightly oblique shearing blade. Postero-internally, there is a small talonid rudiment in B.M. M13075 and S.M. C31347 (more strongly developed in B.M. 29752). Antero-externally, a buttress is developed as in the other molars. A trace of the antero-internal cuspule situated high on the antero-internal paraconid face is present in the least worn specimens.

Anterior to the orbits, the maxillaries have a great height, as is seen in S.M. C30775. The infra-orbital foramen is narrow and slit-like, opening above P^3 (B.M. M25073 and S.M. C30775). S.M. C31347c and d indicate a fairly narrow palatal region.

I^3 is a very small pointed tooth, slightly separated from the canine alveolus (S.M. C30775). The upper canine (S.M. C31347k, S.M. C30775 and B.M. M25073) is a large curved tooth with an ovoid section and a long vertically-striated root. P^1 (B.M. M25073) is double-rooted, elongated antero-posteriorly and situated immediately posterior to the canine; the tooth has a main cusp over the anterior root, and a strong continuous internal cingulum. P^2 is larger than P^1, but otherwise similar; it is separated from P^1 by a gap.

P^3 is separated from P^2 by a gap. This tooth is slightly larger than P^2 (B.M. M25073) and has two roots. The main cusp is crested antero-internally and posteriorly. There is a distinct crested posterior cusp, separated from the main cusp by a cleft, and a prominent internal cingulum.

P^4 (S.M. C31347c and d, and S.M. C30775) has three roots and lies immediately posterior to P^3. There is a strong protocone lobe but no distinct cusp; the transverse width is greater than the antero-posterior length. The large main cusp is separated from a small though distinct posterior cusp by a cleft; there is a small anterior cusp (more developed in B.M. M13075 and S.M. C30775 than in S.M. C31347c and d).

M^1 is much smaller than P^4 and situated immediately posterior to it; the tooth is triangular-shaped, the antero-posterior length being about the same as the transverse width. The crested anterior cusp (fused metacone and paracone) and a crested metastyle form an effective shearing blade; the cusps are separated internally by a small cleft and externally by a shallow valley. There is a small indistinct parastyle in S.M. C31347d; this is better developed in B.M. M13075.

M^2 is very similar structurally but much larger and more trenchant. The crested metastyle is tapered and elongated posteriorly; with the crested metacone/paracone, this forms internally an elongated almost vertical shear plane.

REMARKS. With the exception of B.M. M13075, most of the material listed above, for many years has been referred to the Late Eocene species, *Hyaenodon minor*. The length of the tooth row and the single-rooted P_1 appear to exclude reference to any of the other European species of Late Eocene age (listed in Savage, 1965 : 280); with the present chaotic state in the systematics of the genus, comparison of the Headon specimens with *Hyaenodon minor* seems the most reasonable course.

Cooper (1926) described a new species, *Hyaenodon aimi*, based on a well-preserved mandible from the Lower Headon Beds of Hordle Cliff. In the present work, the holotype (and only specimen) of '*Hyaenodon aimi*' is not considered specifically distinct from the other Headon Beds material. The length of the lower tooth row in the holotype of '*Hyaenodon aimi*' and in the specimens of *Hyaenodon* c.f. *minor* is almost identical (see table of measurements); dimensions of individual teeth in the two species overlap considerably. The only difference in dentition worthy of mention is the presence of a distinct cuspule antero-internal to the paraconid on M_1 and M_2 in *Hyaenodon* c.f. *minor;* this cuspule is indistinct in the holotype of '*Hyaenodon aimi*', but its presence or absence is unlikely to be of any significance.

Cooper (1926) noted the closely similar length of the lower tooth row in '*Hyaenodon aimi*' and the other Headon Beds specimens, but cited as differences the smaller more slender mandible, the closed tooth row and the curved lower margin of the mandible in '*Hyaenodon aimi*.' In particular, Cooper emphasised the differences in mandible depth below M_3 and considered the possibility of this variation being caused by differences in the sex of individuals; he concluded, by comparison with living carnivores, that the discrepancy in dimensions was too great to be accounted for in this way.

It is highly probable that these differences in mandible shape and size are due to variations in individual age. The holotype of '*Hyaenodon aimi*' is of a young individual with only a slightly worn dentition. Nearly all of the remaining Headon Beds specimens of lower dentitions exhibit greater degrees of wear, indicating more mature individuals; in these animals, increasing age has been accompanied by many changes such as a deepening of the mandible, flattening of the lower margin of the mandible and spacing of the premolars.

B.M. M25074 is rather smaller than most specimens, with a curiously small M_2. The specimen may be specifically distinct, but as little is known about intraspecific size variation in Hyaenodon species, it is best grouped at present with the other material. In general aspect, the teeth in B.M. M13075 and B.M. M25075 are slightly more slender and delicate; these specimens may represent females of the species.

TABLE 17

Measurements (in mm) of *Hyaenodon* c.f. *minor*

	P_2		P_3		P_4		M_1		M_2		M_3		P_3–M_3
	a-p	trs	a-p	trs	a-p	trs	a-p	trs	a-p	trs	a-p	trs	a-p
B.M. 29814	—	—	—	—	—	—	—	—	—	—	16·1	7·0	—
B.M. 29752	9·4	4·6	12·2	5·0	—	—	—	—	(10·4)	4·8	(14·1)	—	55·5
B.M. 29752	9·4	4·7	12·3	5·1	12·4	6·4	—	—	(11·4)	—	(14·8)	(6·2)	55·5
S.M. C31347a	—	—	—	—	12·2	6·3	(7·9)	—	10·4	5·0	15·0	6·6	—
S.M. C31347b	9·6	4·7	—	—	12·8	6·1	7·6	4·2	10·5	4·8	14·5	6·3	(57·0)
S.M. C31344	—	—	—	—	12·2	6·1	7·6	4·0	10·0	5·2	—	—	—
S.M. C31346	—	—	11·3	5·0	—	—	—	—	—	—	—	—	—
B.M. M25074	—	—	9·7	5·2	11·2	5·4	7·2	4·1	7·3	4·8	11·9	5·7	45·5
B.M. M13075	9·5	5·9	10·9	5·5	11·4	6·2	8·2	5·0	11·3	6·2	14·8	7·0	56·0
B.M. M13075	10·0	5·6	11·2	5·4	11·6	5·9	8·4	4·7	11·6	5·8	14·6	6·8	56·0

	P^2		P^3		P^4		M^1		M^2		P^4–M^2
	a-p	trs	a-p	trs	a-p	trs	a-p	trs	a-p	trs	a-p
B.M. M25073	7·6	3·6	11·0	5·2	12·4	6·3	—	—	—	—	—
S.M. C31347c	—	—	—	—	—	—	11·3	10·7	—	—	—
S.M. C31347d	—	—	—	—	11·0	10·2	9·8	7·3	(14·0)	9·3	(32·5)
S.M. C30775	—	—	—	—	(12·8)	6·9	10·5	(9·7)	—	—	—
B.M. M25075	11·6	7·1	14·7	8·3	13·2	11·6	10·7	7·9	17·4	10·6	41·5

Order CARNIVORA

Family **MIACIDAE** Cope, 1880

DIAGNOSIS. P^4, M_1 carnassials as in modern carnivores. Post-carnassial teeth more or less tubercular. Metacone smaller than protocone (Matthew, 1909).

REMARKS. The family is recorded from the Middle Palaeocene-Late Eocene of North America; Late Eocene of Europe and Late Eocene–?Early Oligocene of Asia. The group has been traditionally divided into two subfamilies (Simpson, 1945 and Piveteau, 1961): Viverravinae Matthew, 1909 and Miacinae Trouessert, 1885.

Subfamily **VIVERRAVINAE** Matthew, 1909

DIAGNOSIS. Molars $\frac{2}{2}$. Antero-external cusp of P^4 and posterior accessory cusp of P_4 prominent. Elongated oval outline of M^2. M_3^3 absent. Skull much elongated. (Partly from Matthew, 1909).

REMARKS. Distinguished from the other subfamily as follows: in the Miacinae the skull is short or moderately elongated; molars $\frac{3}{3}$ and the antero-external cusp of P^4 and the posterior accessory cusp of P_4 rudimentary or absent.

The Viverravinae contains five genera:

Didymictis Cope, 1875. Middle Palaeocene-Early Eocene; North America.

Ictidopappus Simpson, 1935. Early-Middle Palaeocene; North America.

Protictis Matthew, 1937. (incl. *Simpsonictis* MacIntyre, 1962.). Middle (and Late?) Palaeocene; North America.

Viverravus Marsh, 1872. Early-Middle Eocene; North America. ?Early Oligocene; Asia.

Quercygale Kretzoi, 1945. Late Eocene; Europe.

In 1962, MacIntyre described a new genus *Simpsonictis*. More recently, MacIntyre (1965 : 3544) has separated *Protictis* Matthew, 1937, from *Didymictis* as a distinct genus: *Protictis* was considered to include *Simpsonictis* MacIntyre, 1962.

Genus ***QUERCYGALE*** Kretzoi, 1945

1965 *Humbertia* Beaumont: 142.

DIAGNOSIS. Viverravinae of medium to large size. P^4 with or without parastyle, deuterocone strong and projected. M^1 with strong parastyle, paracone robust and flattened externally, metacone smaller and more conical, no true metaconule but a paraconule present. Protocone near the anterior border bearing two crests. No hypocone. M^2 much smaller than M^1 and very elongated transversely. Lower premolars have a posterior cuspule low and trenchant. M_1 high with a metaconid higher than the paraconid. Talonid short with hypoconid trenchant and dominant. M_2 small with trigonid complete and talonid reduced and trenchant. Symphysis high and short, coronoid process more or less reduced (modified from Beaumont, 1965).

TYPE SPECIES. *Quercygale angustidens* (Filhol, 1872). ?Early Ludian (Quercy Phosphorites); France.

REMARKS. Teilhard de Chardin (1914–15) first recognised the viverravine affinities of *Viverra angustidens* Filhol, placing it in the American genus *Viverravus*. This European material was separated by Kretzoi (1945) as a new genus *Quercygale*. Beaumont (1965) placed '*Viverravus*' *angustidens* into a new genus *Humbertia* and described a new species *Humbertia helvetica* (Rütimeyer, 1862). *Humbertia* Beaumont, 1965, is synonymous with *Quercygale* Kretzoi, 1945 (Beaumont, 1966 : 282).

Quercygale differs from the other genera as follows: in *Viverravus*, the M_2 trigonid is high and the talonid is long with a distinct hypoconulid; M^1 has a hypocone (usually), a paraconule is absent and the P^4 parastyle is invariably present. *Ictidopappus* has upper teeth with a pronounced transverse elongation; the talonid of P_4 is short with a very small cusp and the lower molar talonids are basined. In *Protictis*, the M_1 and M_2 trigonid is higher and the talonid is larger and wider transversely; P_3 and P_4 have a well separated anterior cusp. As observed by Beaumont (1965), *Quercygale* appears closest to *Didymictis* but in this latter genus, the M_1 and M_2 talonid is basined and the P_4 parastyle is invariably present. Beaumont (1965) observed that apart from the absence of M_3, *Quercygale* is very similar to *Tapocyon* Stock, 1934, a miacine from the American Late Eocene. Van Valen (1967) has considered that this presence or absence of M_3 is inadequate for generic distinction, and that *Quercygale* is best considered as a subgenus of *Tapocyon*. Following this, Van Valen has concluded (1967 : 255) that . . . 'the Miacinae can no longer be unambiguously distinguished from the Viverravinae on the basis of the presence of three molars rather than two'.

Three species are recognised here:

Q. angustidens (Filhol, 1872), pl. 17, figs 33–35. Late Eocene (Bartonian-Early Ludian); France.

Q. helvetica (Rütimeyer, 1862), p. 86, pl. 5, fig. 86. Middle Eocene (Lutetian); Switzerland.

Q. hastingsiae (Davies, 1884), p. 433, pl. 15, figs 1-4. Late Eocene (Early Ludian); Britain.

Beaumont (1966) noted that *Miacis? macintyri* Van Valen, 1965, from the Lutetian of Germany, is very similar to *Quercygale helvetica*. Reference of *Miacis? macintyri* to *Quercygale* was supported by Van Valen (1967). The species is not well known (based on an isolated P^4 and M^1) and may well be synonymous with *Quercygale helvetica*.

Depéret (1917) described a new species *Procynodictis euzetensis* (later in the same work described as *Viverravus euzetensis*) from the Early Ludian of France. This species was considered by Gauthier & Favre (1948) to fall within the range of variation of '*Viverravus angustidens*'. This latter view was followed by Beaumont (1965 : 143) who recorded *Procynodictis euzetensis* as a synonym of *Humbertia angustidens*. Although the holotype of *Procynodictis euzetensis* has not been examined and Depéret's illustrations (1917, text fig. 2; pl. 24, figs 3–6) make precise comparison difficult, *Procynodictis euzetensis* is synonymised with *Humbertia angustidens* in the present work, on the authority of Gauthier & Favre, and Beaumont.

Quercygale hastingsiae (Davies, 1884)

(Pl. 6)

1884 *Viverra hastingsiae* Davies: 433, pl. 15, figs. 1–4.
1885 *Viverra hastingsiae* Davies; Lydekker: 100, figs 11–12.
1915 *Viverravus angustidens* (Filhol); Teilhard de Chardin (partim): 117.
1917 *Viverravus hastingsiae* (Davies); Depéret: 248.
1965 *Humbertia angustidens* (Filhol); Beaumont (partim): 143.

DIAGNOSIS. About the same size as *Q. angustidens*. M_1 trigonid somewhat wider and larger than talonid, with fairly blunt anterior apex; talonid larger than that of *Q. angustidens* with squared outline. Outline of upper teeth rounded; internal lobe of P^3 large; posterior margin of M^1 with strong embayment.

HOLOTYPE. B.M. 30203. Skull and mandible in occlusion. Badly crushed and damaged. The outline of the skull is preserved in fine greenish sand matrix, but only the lower part is distinct and relatively undamaged. The right and left halves of the skull have been displaced by crushing along the palatal sutures; the occluded mandibular rami are also similarly displaced relative to each other. To facilitate examination, the posterior part of the right ramus has been removed (in the past) from its original occluded position. The removed right ramus shows P_3–M_2, the exposed right maxilla and premaxilla, I–C–M^2. The upper and lower teeth anterior to P_3^3 are damaged, displaced and partly obscured by matrix. Described and figured, Davies, 1884 : 433, pl. 15, figs 1–4. Lydekker, 1885a : 100, figs 11–12. From Lower Headon Beds (Mammal/Crocodile Bed), Hordle Cliff. The only known specimen from the Headon Beds.

Description. P_3 is rectangular in outline and elongated antero-posteriorly, with a slight anterior narrowing. The anterior margin is squared, the posterior margin more rounded. There is a large crested central cusp and a prominent talonid which bears a small cusp. A slight postero-external and antero-internal cingulum is present. P_4 is generally similar to P_3 but much larger, and the anterior narrowing is more prominent. The talonid bears an antero-posteriorly aligned crestiform cusp and is basined internally.

The largest tooth is M_1; this has a stout bulbous trigonid which is much wider and longer than the talonid. The protoconid, the largest cusp, is opposite the metaconid; both cusps are anteriorly and transversely crested. The paraconid, the smallest trigonid cusp, is crestiform with its internal edge strongly internal in position. There is a short but wide antero-external cingulum. The small talonid is structurally similar to P_4; the internal region is slightly basined and there is an antero-posteriorly aligned crestiform cusp. M_2 is very short antero-posteriorly. The trigonid is almost as wide transversely as the talonid of M_1, with very low cusps; the protoconid is largest and slightly anterior to the metaconid. A low curved crest running from the internal paraconid to the protoconid, forms the squared anterior tooth margin. The antero-external part of this crest is badly worn; it may represent the site of a small cusp. The talonid, small and narrowing posteriorly, is well worn and shows no evidence of any cusps.

The upper teeth anterior to and including P^2 have been much displaced from their original positions. One upper incisor is preserved; it is small and simple. The upper canine is large and curved with a strong root. P^1 is embedded in matrix; it is smaller than the incisor with a single central cusp. The anterior region of P^2 is missing. The tooth has a central major cusp but is larger and more elongated antero-posteriorly than P^1. P^3 is strongly elongated antero-posteriorly and very much larger than P^2. The tooth narrows anteriorly and is dominated by a large central crested cusp. Posteriorly there is a low rounded separated cusp and a postero-external shelf-like cingulum. P^4 is triangular-shaped in outline and much larger than P^3. The tooth is dominated by a large central crested paracone; antero-externally this falls as a crest towards a low rounded parastyle. There is a low rounded protocone which is larger than the parastyle. The anterior margin between parastyle and protocone is strongly embayed. The crestiform metacone is separated from the paracone by a deep cleft which continues externally as a narrow valley; these cusps together form a sharp oblique postero-internal shearing edge. There is a small distinct antero-external cingulum and a faint postero-external cingulum.

M^1 is the same width transversely as P^4. The metacone is directly posterior to the larger paracone; a posterior metacone crest curves antero-externally along the external tooth margin to the parastyle. The crested protocone is crescentic in shape, an anterior crest running antero-externally towards the paracone; a low paraconule is developed on this crest just antero-internal to the paracone. The parastylar area extends externally as a wing which is separated from the postero-external area by a small embayment. The parastyle is crestiform; it is joined to an external paracone crest. There is a distinct internal and antero-internal cingulum.

M^2 is much smaller than M^1 and a little smaller than P^3. The ovoid tooth lies obliquely in the tooth row. The antero-external margin is in contact with M^1 just posterior to the M^1 metacone. The crown of the tooth is badly damaged and no details can be discerned.

REMARKS. Teilhard de Chardin (1915 : 117, footnote 1) considered that '*Viverravus*' *hastingsiae* was synonymous with '*Viverravus*' *angustidens*. Depéret (1917 : 248) recorded several differences, on the basis of which he believed the two species to be distinct. Gauthier & Favre (1948 : 116) emphasised the larger M$_1$ talonid of '*Viverravus*' *hastingsiae* but were uncertain whether this merited specific separation. More recently Beaumont (1965 : 143) on the evidence of the more elongated M$_1$ talonid, considered '*Humbertia*' *hastingsiae* as a distinct subspecies of '*Humbertia*' *angustidens*. Depéret's view is followed here. In addition to the considerably more elongated talonid of M$_1$, the P^3 of *Quercygale hastingsiae* (from comparison with illustrations of *Q. angustidens*) has a smaller internal heel as Depéret observed. Although this single specimen from the Headon Beds may be aberrant, it seems reasonable at present to regard it as specifically distinct.

TABLE 18

Measurements (in mm) of *Quercygale hastingsiae*

	P_3		P_4		M_1		M_2	
	a-p	trs	a-p	trs	a-p	trs	a-p	trs
B.M. 30203	7·0	2·8	9·1	3·7	9·7	6·2	5·1	3·6
	P^3		P^4		M^1		M^2	
	a-p	trs	a-p	trs	a-p	trs	a-p	trs
B.M. 30203	7·8	—	11·3	—	6·7	—	—	—

IV. CORRELATION AND AGE OF THE HEADON BEDS

Although there is general agreement concerning the broad correlation of Upper Eocene and Lower Oligocene deposits in Europe, no unanimity has been reached yet regarding the detailed correlation of marine and non-marine sediments in the different depositional basins. One particular problem is the exact siting of the Eocene/Oligocene boundary. The situation is hindered by a confused stage and substage terminology, which despite many recent attempts at clarification by authors, has still to be resolved.

It is not intended here to present a critical review of this problem, detailed aspects of which have been considered recently by Rey (1964), Krutzsch & Lotsch (1964), Blondeau, Cavelier, Feugueur & Pomerol (1965), Thaler (1966), Denizot (1968), Cavelier (1968), Curry, Gulinck & Pomerol (1969) and others. The complete mammalian fauna of the Headon Beds has not yet been studied in detail, and authoritative use of the mammals in correlation and dating is clearly premature. Nevertheless, in view of the importance of the Headon Beds in current stratigraphical research, some interim conclusions are presented here.

The exact age of the Headon Beds and indeed of most of Forbes' 'Fluvio-marine series' has long been controversial. The uppermost beds of the British succession, the Hamstead Beds, are generally accepted to be Oligocene in age. No unanimity has been reached regarding the age of the underlying Bembridge, Osborne and Headon Beds. Three schemes have been proposed in the past for the age of the Headon Beds; two schemes are supported currently by European stratigraphers and palaeontologists, but the third, that proposed by Reid & Strahan (1889) is now obsolete.

Reid & Strahan (1889) and Arkell (1947) considered that the Lower, Middle and Upper Headon Beds were Oligocene (Lattorfian of Arkell) and the underlying Barton Beds were uppermost Eocene. The Eocene/Oligocene boundary lay at the base of the Lower Headon Beds. This view, in which is emphasised the general change from marine to brackish and freshwater conditions at the beginning of Lower Headon times, has not found further support.

In a currently held view, supported traditionally by most British workers, the Lower Headon Beds are considered as uppermost Eocene (Bartonian) and the Middle and Upper Headon Beds are Oligocene (Lattorfian, Tongrian). The Eocene/Oligocene boundary is placed, therefore, at the base of the Middle Headon Beds. This view, based on correlation by mollusca and foraminiferida of the Middle Headon Brockenhurst Bed with the type Lattorfian (Lower Oligocene) of Germany, has been adopted by Wrigley & Davies (1937), Bhatia (1955), Denizot (1957, 1968), Curry (1958a, 1966), Chandler (1961a, 1963), Rey (1964), Franzen (1968) and others.

In the second currently supported arrangement, the Lower, Middle and Upper Headon Beds are placed together with the Barton Beds in the Upper Eocene (Lower Ludian). This was adopted by Stehlin (1910) and followed more recently by Krutzsch & Lotsch (1964), Blondeau, Cavelier, Feugueur & Pomerol (1965), Thaler (1966) and Cavelier (1968). In this scheme, the Eocene/Oligocene junction is placed at some position above the Upper Headon Beds. Stehlin (1910) on the basis of what he believed to be a fundamental break in the mammal faunas ('grande coupure'), considered that the Eocene/Oligocene junction in Britain should be placed at the base of the Hamstead Beds; this has been followed more recently by Krutzsch & Lotsch (1964), Blondeau *et al* (1965) and Cavelier (1968). Thaler (1966) preferred to place the boundary at the base of the Bembridge Beds.

Stehlin (1910) compared the mammalian fauna of St.-Hippolyte-de-Caton (=Euzet-les-Bains) with the Lower Headon Beds, considering them Lower Ludian in age.

The same faunas were compared by Depéret (1917) who also assigned them a Lower Ludian age. Stehlin (1910) also compared the mammalian fauna of Montmartre with a similar fauna from the Bembridge Limestone; he considered these faunas to be Upper Ludian in age. According to Stehlin (1910) the fauna from the Bembridge Marls was similar to that from the Bembridge Limestone. He observed that the Upper Ludian (Bembridge Beds) fauna differed from that of the Lower Ludian (Lower Headon Beds) fauna by the extinction of several species and the arrival of several forms unknown in the Lower Ludian. Stehlin's correlations of the Lower Ludian faunas of Euzet-les-Bains with the Lower Headon Beds, and the Upper Ludian faunas of Montmartre with the Bembridge Limestone, have now become well established.

Recently, Thaler (1965, 1966) proposed to replace the old classification by a series of seven zones defined by theridomyids. Although some of Thaler's zones transgress the traditional stratigraphical subdivisions, the Euzet zone, Montmartre zone and Ronzon zone correspond exactly with the Lower Ludian, Upper Ludian and 'Sannoisian' respectively.

Stehlin (1910) noted that as the faunas of the beds above the Lower Headon Beds and below the Bembridge Limestone were poorly known, it was not possible in Britain to determine the precise junction of the Lower and Upper Ludian faunas. More recently, Krutzsch & Lotsch (1964) grouped the Upper Headon Beds and Osborne Beds in the Montmartre zone with the Bembridge Beds; for them, the junction of Lower and Upper Ludian faunas lay at the base of the Middle Headon Beds.

The mammalian fauna obtained recently from the Upper Headon Beds appears to be similar to that from the Lower Headon Beds and apparently distinct from the Bembridge fauna. While the sample from the Upper Headon Beds is clearly still incomplete, the Upper Headon Beds, on present evidence, should be grouped, at least provisionally with the Lower Headon Beds in the Upper Eocene (Lower Ludian). The Upper Headon fauna should be placed in the Euzet zone, rather than the Montmartre zone as suggested by Krutzsch & Lotsch (1964). It follows that, on the basis of the mammalian faunas, the traditional British practice of siting the Eocene/Oligocene boundary at the base of the Middle Headon Beds, cannot be sustained. This present view is in agreement with Martini (1970) whose study of calcareous nannoplanckton from the Brockenhurst Bed, has indicated that the Brockenhurst Bed is uppermost Eocene in age, and not equivalent to the type Lattorfian (Lower Oligocene).

The Eocene/Oligocene boundary therefore, must be situated at some position above the Upper Headon Beds. Owing to the poorly known mammalian fauna, the exact stratigraphical position of the overlying Osborne Beds is uncertain at present. However, study of this fauna, together with the fauna of the Bembridge Beds, currently in progress by Mr A. Insole at the University of Bristol, may clarify this situation.

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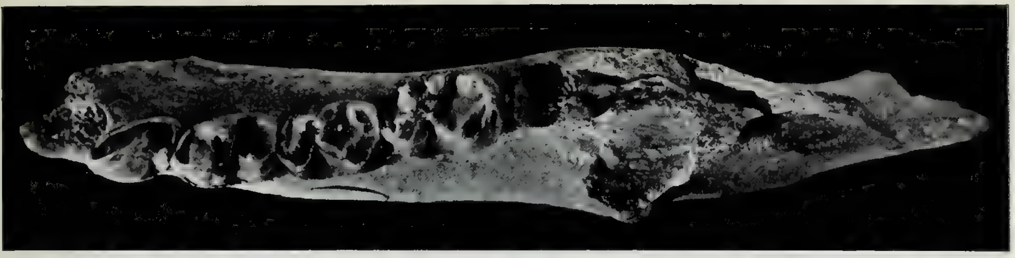
PLATE 1

×2 approx.

Adapis magnus Filhol. Lower Headon Beds, Hordle Cliff

FIGS 1–2. Fragmentary left mandibular ramus with P_3–M_2. B.M. M10260. Fig. 1. Occlusal view. Fig. 2. External view.

FIG. 3. Fragmentary left maxilla with P^2–P^3, M^1–M^3. B.M. M3572. Occlusal view.



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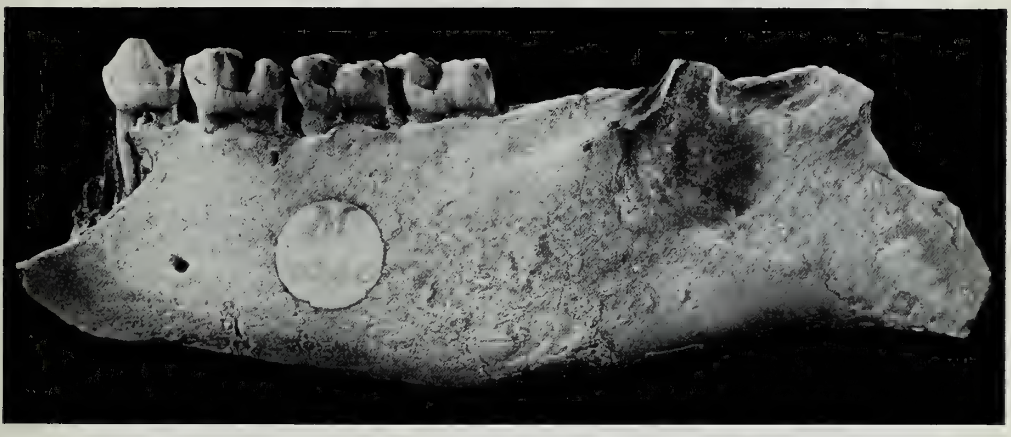

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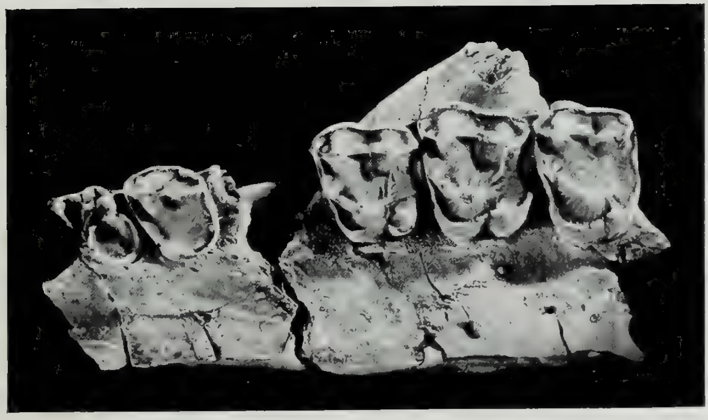

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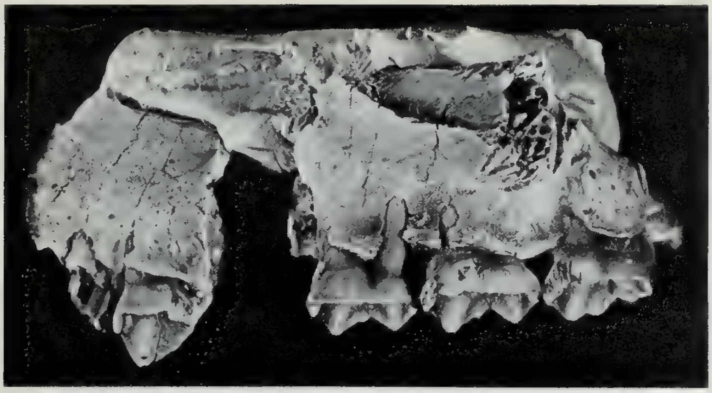
PLATE 2

×2 approx.

FIG. 1. ***Adapis magnus*** Filhol. Fragmentary left maxilla with P^2–P^3, M^1–M^3. B.M. M3572; External view. Specimen supported in plasticine. Lower Headon Beds, Hordle Cliff.

FIGS 2–3. ***Adapis parisiensis*** (Blainville). Fragmentary associated mandibular rams. Right ramus with P_2–M_1, M_3, left ramus with M_1–M_3. F.C.S. 7. Upper Headon Beds, Headoi. Hill. Fig. 2. Occlusal view of both rami. Fig. 3. External view of right mandibular ramun



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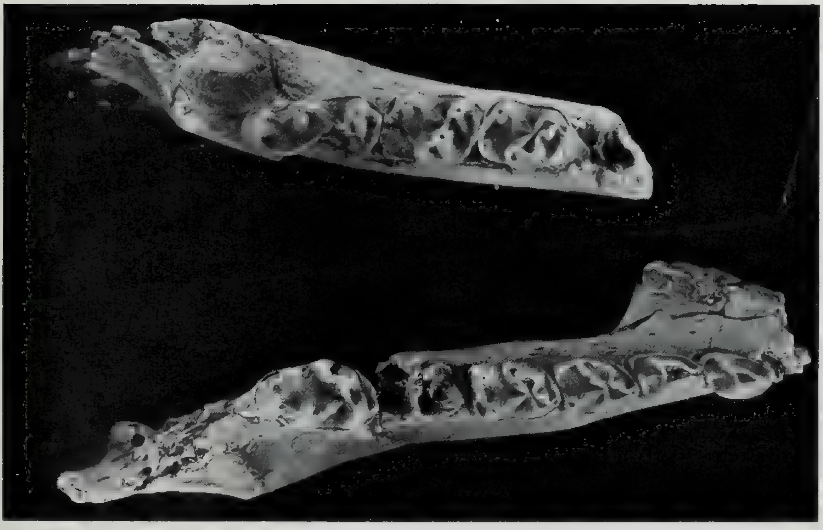

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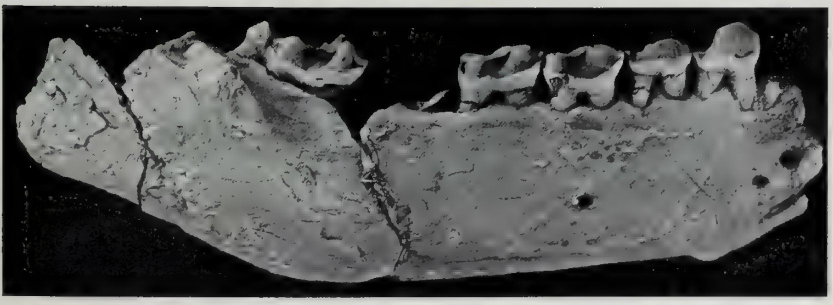


3

PLATE 3

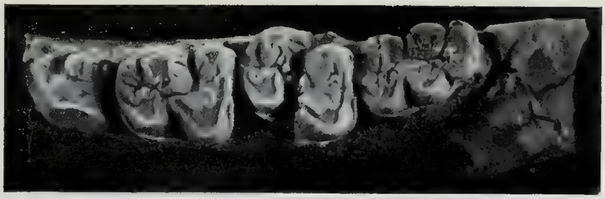
×4 approx.

Microchoerus erinaceus Wood. Holotype (B.M. 25229).

Lower Headon Beds, Hordle Cliff

FIGS 1–2. Fragmentary left mandibular ramus with P_4–M_3. B.M. 25229 (1). Wax reconstruction of anterior and posterior regions not illustrated. Fig. 1. Occlusal view. Fig. 2. External view.

FIG. 3. Palatal fragments with an almost complete upper dentition. B.M. 25229 (2). Occlusal view. Right I^2 is a plaster reconstruction.



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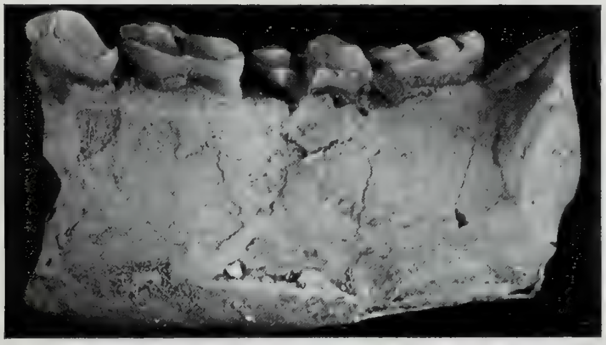

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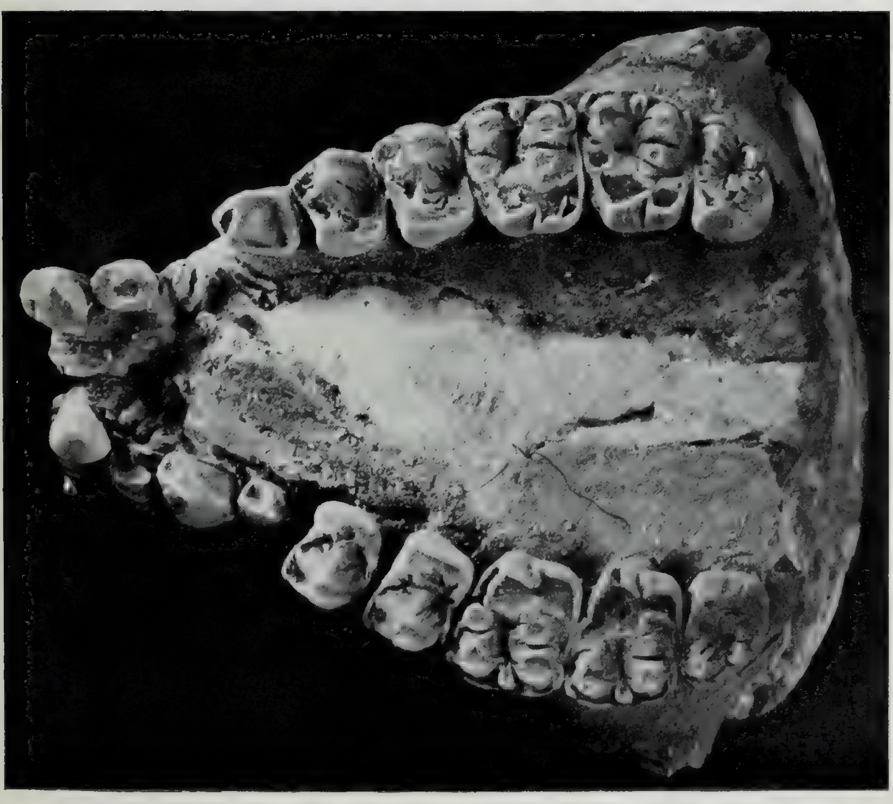

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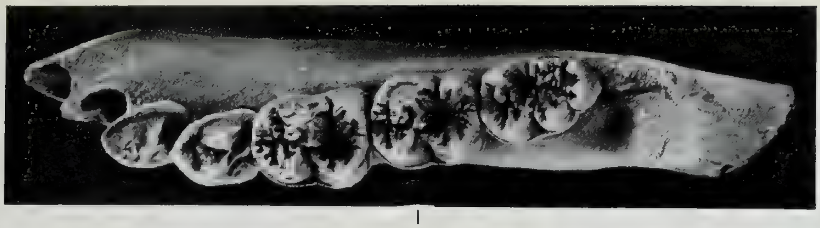
PLATE 4

×4 approx.

Microchoerus erinaceus Wood. Lower Headon Beds, Hordle Cliff

FIGS 1–2. Fragmentary left mandibular ramus with P_3–M_3. S.M. C9681. Fig. 1. Occlusal view. Fig. 2. External view.

FIG. 3. Fragmentary left mandibular ramus with M_1–M_3 and complete posterior region. External view. S.M. C9672.



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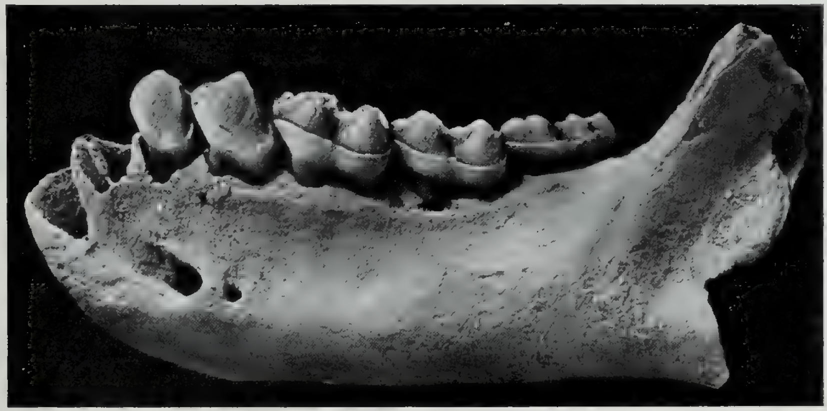

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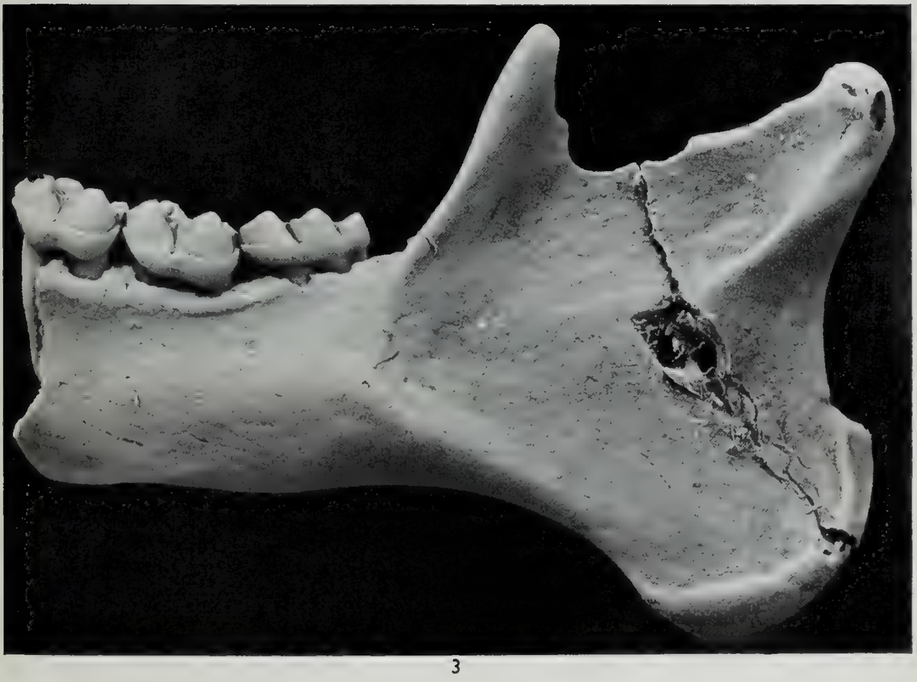

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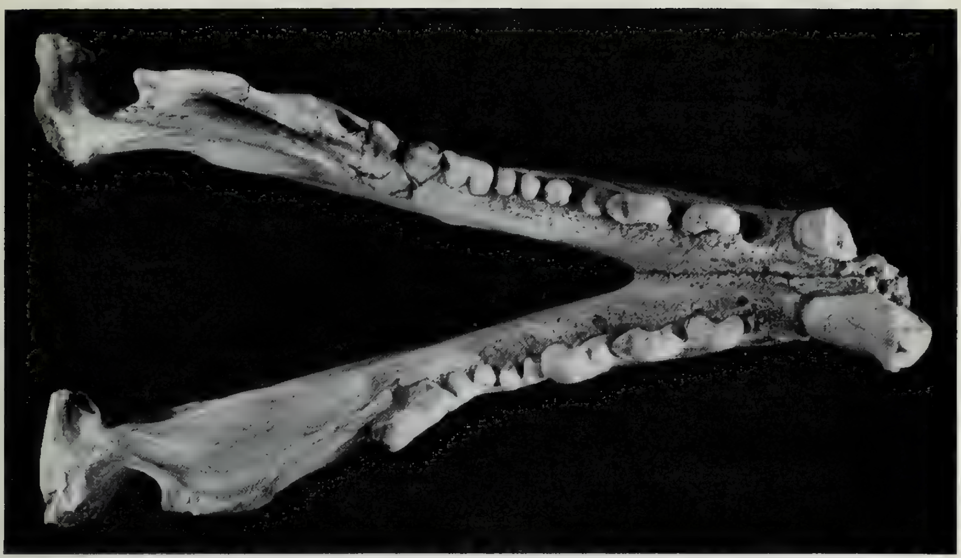
PLATE 5

Hyaenodon c.f. ***minor*** Gervais

FIGS 1–2. Mandible with C, P_2–M_3 of both sides. B.M. 29752 ×0·8 approx. Lower Headon Beds, Hordle Cliff. Fig. 1. Occlusal view of both rami. Fig. 2. External view of right ramus.

FIGS 3–4. Fragmentary left maxilla with P^2–M^2. B.M. M25075 ×1 approx. Upper Headon Beds, Headon Hill. Fig. 3. Occlusal view. Fig. 4. External view.



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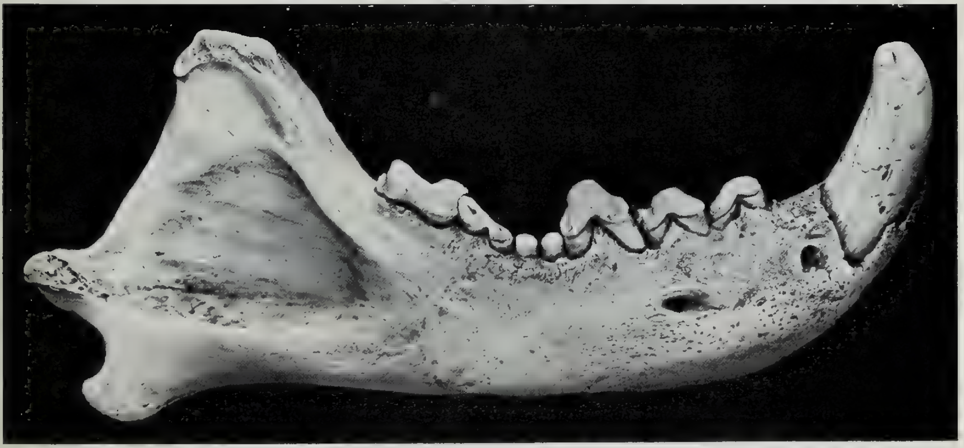

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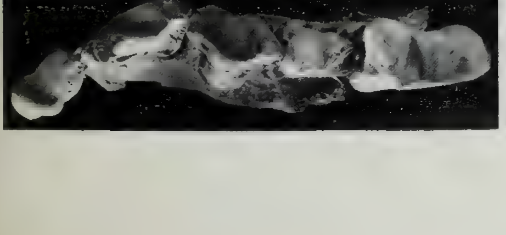

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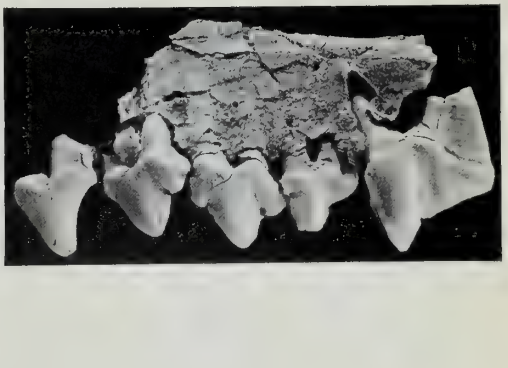


PLATE 6

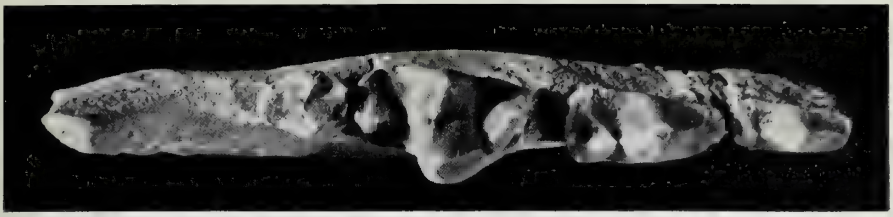
×2·5 approx.

Quercygale hastingsiae (Davies). Holotype (B.M. 30203)

Lower Headon Beds, Hordle Cliff

FIGS 1–2. Fragmentary right mandibular ramus with P_3–M_2. Fig. 1. Occlusal view. Fig. 2. External view.

FIG. 3. Right P^3–M^2; Occlusal view.



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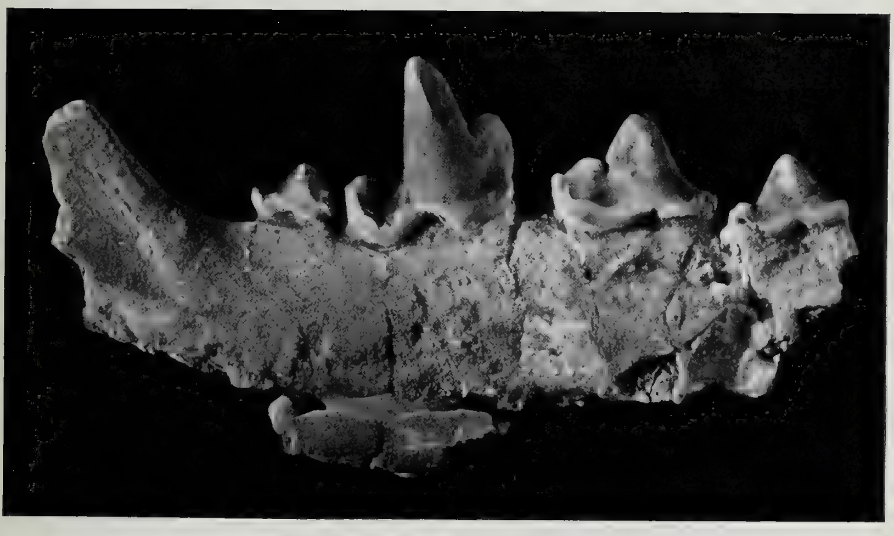

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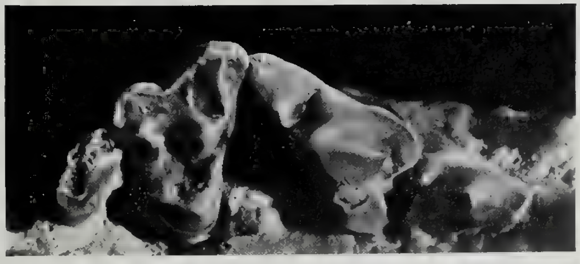

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H. L. ABBASS

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GEOLOGY Vol. 23 No. 2
LONDON : 1973

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BY

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By H. L. ABBASS

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LIST OF GENERA AND SPECIES

Family **PROCERITHIIDAE**
- Genus *Nerineopsis* Cossmann, 1906
    - *N. claxbiensis* sp. nov.
    - *N. aculeatum* (Sharman & Newton)
    - *N. subattenuatum* d'Orbigny
    - *N. coxi* sp. nov.
    - *N. melburiensis* sp. nov.
    - *N. cuckhamsliensis* (Woods)
    - *N. adeli* sp. nov.
- Genus *Cirsocerithium* Cossmann, 1906
    - ? *C. kirkaldyi* sp. nov.
    - *C. subspinosum* (Deshayes)
    - ? *C. nooryi* sp. nov.
- Genus *Nudivagus* Wade, 1917
    - *N. morrisi* sp. nov.
- Genus *Bathraspira* Cossmann, 1906
    - *B. tecta* (d'Orbigny)
    - *B. shanklinensis* sp. nov.
    - *B. cleevelyi* sp. nov.
    - *B. brightoni* sp. nov.
- Genus *Metacerithium* Cossmann, 1906
    - *M. trimonile* (Michelin)
    - *M. ornatissimum* (Deshayes)
    - *M. turriculatum* (Forbes)
    - *M.* sp. nov.

Genus *Cimolithium* Cossmann, 1906
    C. ascheri Wollemann
    C. aff. *eleanorae* Allison
Genus ? *Rhabdocolpus* Cossmann, 1906
    ? *Rhabdocolpus* ? *clementinum* (d'Orb.)
    ? *Rhabdocolpus forbesianum* (d'Orbigny)
    ? *Rhabdocoplus melvillei* sp. nov.

Family ? **PROCERITHIIDAE**
Genus *Uchauxia* Cossmann, 1906
    U. wisei sp. nov.
    U. badri sp. nov.
    U. sp. nov.

Family **CERITHIIDAE**
Genus ? *Campanile* Bayle, 1884
    C. cenomanica sp. nov.
Genus *Exechocirsus* Cossman, 1906
    E. saundersi (Woods)
    E. aff. *subpustulosus* Pčhelincev

Family ? **CERITHIIDAE**
Genus *Ageria* nov.
    A. gaultina sp. nov.
    A. costata (J. de C. Sowerby)

Family **CERITHIOPSIDAE**
Genus *Cerithiella* Verrill, 1882
    C. devonica sp. nov.
    C. atherfieldensis sp. nov.
Genus *Seila* Adams, 1861
    S. iglali sp. nov.
Genus *Orthochetus* Cossmann, 1889
    O. hantoniensis sp. nov.
    ? *O. helmyi* sp. nov.
    ? *Orthochetus* sp. nov.

SYNOPSIS

Cretaceous Cerithiacea are described from principally two formations, the Crackers Bed in the Lower Greensand (Aptian) and the Gault Clay (Albian), comprising 14 genera and 38 species (23 of which are new). A new genus *Ageria* is erected and is provisionally included in the Cerithiidae. Aspects of the phylogeny of the Cerithiacea are discussed.

I. INTRODUCTION

This paper is the second resulting from a study of British Cretaceous gastropods, and is a revision of part of the work undertaken at Imperial College, University of London, during 1954–1956 for the degree of Ph. D. The families Procerithiidae, Cerithiidae and Cerithiopsidae (superfamily Cerithiacea) are sparsely represented in the British Cretaceous. Cox (1960) has recorded the limited literature describing British gastropods of this age. Most of the material described in this paper comes from old collections now in the major museums. Unfortunately, in many cases, nothing is known of the precise horizons and localities from which the specimens were collected, and some of the exposures no longer exist. Moreover, the specimens come from relatively few localities; 57% of the total of 62 Aptian specimens come from exposures on the Isle of Wight and of these, 52 were found at Atherfield, and include 39 from the Lower Greensand, Crackers Bed, exposed at that locality. Similarly, 82% of Albian material comes from Folkestone, Kent, and 11% from Blackdown, Devon.

Sixteen of the 38 species described are only represented by single specimens and this is ample evidence of the scarcity of such fossils. In only eight cases are specimens of the same species recorded for more than one locality; three examples are *Metacerithium turriculatum*, *Exechocirsus saundersi* and *Nerineopsis cuckhamsliensis*.

This sparsity of the gastropod fauna reflects the aragonite composition of their shells (see Kennedy, 1969 : 462–465). They are most prolific where the shells have become silicified as at Blackdown, Devon; or where they have been preserved in hard rock bands ('Hard grounds') such as the Chalk Rock (see Wood, 1969 : 44 & 49–50); or in concretions, e.g. the Crackers Bed, I.O.W.; or in ironstone nodules such as those of Groups 14 & 15 of the Ferruginous Sands, I.O.W.

In an earlier paper (Abbass, 1961), I attempted to review the origin of the families discussed here and also to evaluate the significance of morphological and ornamental characters in their development. Although the present paper reveals numerous problems in classifying these Cretaceous fossils, it is hoped that it makes some contribution towards the documentation of Mesozoic gastropods that Sohl (1968: 1364) regards as a necessary preliminary to the more sophisticated analysis of the Class at this period. Once the rudimentary data is available, the stratigraphical use of gastropods that he envisages may be realized. His own work, showing the use of ornament changes in the Aporrhaidae (1960) and his recognition of the delineation of faunal provinces from the distribution of North American gastropods (1969), illustrates such potential usage.

II. ACKNOWLEDGMENTS

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III. THE STRATIGRAPHICAL DISTRIBUTION OF THE SPECIES DESCRIBED

Senonian. The Upper Chalk has yielded a single specimen, *Nerineopsis adeli* sp. nov. from the Campanian, Springbank, nr. Coagh, Co. Derry, Northern Ireland.

Turonian. The Chalk Rock, at the base of the Holaster planus Zone, has provided a number of specimens of *Exechocirsus saundersi* (Woods): Missenden and Hitchin, Herts.; Medmenham and Latimer, Bucks.; Kensworth Quarry, Beds.; Cuckhamsley, Wilts. The last locality has also yielded *Nerineopsis cuckhamsliensis* (Woods).

Cenomanian. Schloenbachia varians Zone: *Metacerithium ornatissimum* (Deshayes) [Berks. and Bucks.].

Cenomanian (zonal details not known): ?*Cirsocerithium nooryi* sp. nov. (Ditchling, Sussex); *Cimolithium* aff. *eleanorae* Allison, (Charlton Bay, Devon); ?*Campanile cenomanica* sp. nov. [Devon]; *Nerineopsis melburiensis* sp. nov. (nr. Shaftesbury, Dorset); *Metacerithium ornatissimum* (Desh.), (Hamsey, Sussex and Burham and Dover, Kent).

Albian. Upper Albian: *Seila iglali* sp. nov. (nr. Honiton, Devon); *Exechocirsus* aff. *subpustulosus* Pčhelincev (Haldon, Devon); *Ageria costata* (J. de C. Sowerby) (Peak Hill, nr. Sidmouth, Devon); *Ageria gaultina* sp. nov. (Osmington, Dorset).

Upper Greensand, Blackdown, Devon: *Bathraspira ?brightoni* sp. nov.; *Cerithiella devonica* sp. nov., *Ageria costata* (J. de C. Sow.); *Uchauxia badri* sp. nov.

Gault Clay, Folkestone, Kent: Bed 1 (vii) intermedius Sub-zone, *Nerineopsis coxi* sp. nov.; horizon unrecorded, *Cirsocerithium subspinosum* (Deshayes), *Bathraspira tecta* (d'Orbigny), *Bathraspira fouadi* sp. nov., *Bathraspira brightoni* sp. nov., *Nerineopsis coxi* sp. nov., *Metacerithium trimonile* (Michelin), *Metacerithium*? sp. nov., *Uchauxia* sp. nov., ?*Orthochetus helmyi* sp. nov., *Ageria gaultina* sp. nov.

Lower Albian, Leymeriella regularis Subzone of the L. tardefurcata Zone: *Bathraspira tecta* (d'Orbigny) (Leighton Buzzard), *Bathraspira cleevelyi* sp. nov. (? Wrotham or Leighton Buzzard).

Aptian. Upper Aptian, Ferruginous Sands, Parahoplites nutfieldensis Zone, Isle of Wight: *Bathraspira shanklinensis* sp. nov. (Shanklin and Sandown), *Nudivagus morrisi* sp. nov., *Cirsocerithium kirkaldyi* sp. nov.

Lower Aptian, Deshayesites callidiscus Subzone of D. forbesi Zone; Crackers Bed, Atherfield, Isle of Wight: ?*Rhabdocolpus clementinum* (d'Orbigny), ?*Rhabdocolpus forbesianum* (d'Orb.), ?*R. melvillei* sp. nov., *Metacerithium turriculatum* (Forbes) *Cerithiella atherfieldensis* sp. nov., *Nerineopsis subattenuatum* (d'Orb.).

Lower Aptian, Deshayesites kiliani Subzone of D. forbesi Zone, Lower Lobster Bed: ?*Rhabdocolpus clementinum* (d'Orb.) (Atherfield, Isle of Wight).

Lower Aptian, Deshayesites forbesi Zone: *Metacerithium turriculatum* (Forbes) [Surrey and Kent].

Lower Aptian, Atherfield Clay Series: ?*Rhabdocolpus forbesianum* (d'Orb.), *Metacerithium turriculatum* (Forbes) [Surrey].

Lower Aptian, Atherfield, Isle of Wight: *Orthochetus hantoniensis* sp. nov.

NEOCOMIAN. Speeton Clay, Beds C6 to C8 (Hauterivian): *Nerineopsis aculeatum* (Sharman & Newton).

Speeton Clay, Beds D1 to B (Valanginian—Berriasian/Barremian): *Cimolithium ascheri* (Wollemann).

Claxby Ironstone and Claxby Beds (Valanginian—Hauterivian): *Uchauxia wisei* sp. nov. (Nettleton, Lincs.), *Nerineopsis claxbiensis* sp. nov.

IV. CHANGES IN GENERIC OR SPECIFIC ASSIGNMENTS

The following are the changes in generic or specific assignments of previously described species mentioned in the text.

Old assignment	New assignment
Cerithium aculeatum Forbes, 1845	*Nerineopsis aculeatum* (Sharman & Newton)
Cerithium attenuatum Forbes, 1845	*Nerineopsis*
Cerithium gottfriedi Wollemann, 1900	*Nerineopsis*
Cerithium frickei, Wollemann, 1906	*Nerineopsis*
Cerithium cuckhamsliense Woods, 1896	*Nerineopsis*
Cerithium turriculatum Forbes, 1845	*Metacerithium*
Cerithium mosense Buvignier, 1852	*Metacerithium ornatissimum* (Desh.)
Cerithium delpeyae Collignon, 1949	*Metacerithium*
Cerithium ascheri Wollemann, 1908	*Cimolithium*
Cerithium sanctaecrucis Pictet & Campiche, 1864	*Cimolithium*
Cerithium terebroides d'Orbigny, 1842	?*Cimolithium*
Cerithium ricordeanum Cotteau, 1854	?*Cimolithium*
Cerithium inauguratum, Stoliczka, 1867	?*Campanile*
Cerithium hispidulum Stoliczka, 1867	not *Cimolithium*
Cerithium gallicum d'Orbigny, 1843	not *Cimolithium*
Cerithium clementinum d'Orbigny, Forbes, 1845	?*Rhabdocolpus*
Cerithium forbesianum d'Orbigny, 1850 = *Uchauxia forbesiana* (d'Orbigny) Cossmann	?*Rhabdocolpus*

Cerithium phillipsi Leymerie, 1842	*Uchauxia*
Cerithium saundersi Woods, 1896	*Exechocirsus*
Cerithium pustulosum d'Orbigny 1843 (non Sowerby)	*Exechocirsus*
Cerithium navasi Vidal, 1917	*Exechocirsus*
Turritella costata J. de C. Sowerby, 1827	*Ageria*
Cerithium binodosum Roemer, in Frič, 1894	*Ageria*
Turritella angustata d'Orbigny, 1850	?*Ageria*
Cerithium hector d'Orbigny, 1850 in Guéranger, 1867	?*Ageria*
Tympanotonus (*Exechocirsus*)	*Exechocirsus*
Procerithium (*Rhabdocolpus*)	*Rhabdocolpus*

V. SYSTEMATIC DESCRIPTIONS

Class *GASTROPODA*

Subclass *PROSOBRANCHIA*

Superfamily **CERITHIACEA**

Family **PROCERITHIIDAE**

Haas (1953 : 212) has shown that the accepted subdivisions of this family, i.e. Cossmann (1906) and Wenz (1940) do not represent the true phylogenetic relationships within the group. He pointed out that the close similarity of *Protofusus* Bonarelli, *Paracerithium* Cossmann and *Rhabdocolpus* Cossmann conflicted with their being members of different subfamilies. Before their correct affinities can be determined, it is necessary to investigate Triassic faunas in more detail.

In this paper, the genera of the Procerithiidae are not divided into subfamilies. Cretaceous species of the following genera are described: *Nerineopsis*, *Nudivagus*, ?*Rhabdocolpus*, *Cirsocerithium*, *Bathraspira*, *Metacerithium* and *Cimolithium*. *Uchauxia*, Cossmann, 1906 was originally included in the subfamily Metacerithinae, but it is pointed out below (p. 146) that the true position of this genus is dependent on the apertural shape of its type species *U. peregrinorsa* and until this has been ascertained, its inclusion in the Procerithiidae remains provisional.

While describing the British Cretaceous members of this family, the difficulties experienced in assigning species to particular genera revealed the limitations of existing diagnostic characters of ornament, aperture, suture and whorl shape in distinguishing the various forms. These inherent problems underline the need for a modern revision of the family.

Genus ***NERINEOPSIS*** Cossmann, 1906

Type species. By original designation, *Cerithium davoustianum* Cotteau, 1854.

Remarks. It is necessary to rely on Cossmann's interpretation of the type species *N. davoustiana* (Cotteau) for the diagnostic characters of the genus, as this species is seldom represented in collections. Peron's figure (Peron, 1902, pl. 4, fig. 6) is rather stylized and does not show the ornament change between early and late whorls that is apparent from Cossmann's figure (1906: pl. 6, figs 9–11). Many of the species referred here to *Nerineopsis* are extremely small and this could be a reason for the poor representation of the genus in collections.

There is considerable variation in ornament both within the genus and within the species, but owing to the limited amount of material available it is not possible to evaluate the importance of this.

The three Upper Cretaceous species that are assigned below to this genus: *melburiensis* (Cenomanian); *cuckhamsliensis* (Turonian) and *adeli* (Campanian), are all very large in comparison to the normal size attained by *Nerineopsis*. Yet any suggestion, that the dimensions of such species may indicate a general increase in size within the genus at this time, is not supported by the other Upper Cretaceous examples listed by Cossmann (1906 : 35) in his original description of the genus, e.g. *C. sarthacense* d'Orbigny (Cenomanian) and *C. chargense* Quaas (1902, pl. 26, fig. 25) (given as Danian but now recognised as Maastrichtian), for both are quite small. However, the resemblance of these larger gastropods, in shell form, whorl outline and ornament to *Nerineopsis*, indicates that they are probably congeneric.

Nerineopsis claxbiensis sp. nov.

(Pl. 1, fig. 13)

Diagnosis. Slender, turriculate shell; ornament of three smooth spiral cords on adapical half of whorl, and smooth lower half and an abapical carina.

Material. BM(NH) GG 5612, C. W. Wright collection, Claxby Beds, Valanginian to Hauterivian, Nettleton, Lincolnshire.

Description. Small, turriculate shell, with narrow spire. Moderately deep linear suture. Whorls very slightly concave in outline with an anterior carina.

Early whorls ornamented by four smooth spiral cords. The anterior one is the most prominent and on later whorls this develops into a smooth anterior carina. Two spiral cords occur close to the adapical part of the whorl and these are separated by an interspace almost equal to their width. The third cord occurs towards the centre of the whorl side, while the area between this and the abapical carina is without ornament of any kind. On the last whorl it is possible to see that an astragal occurs below the carina and that this delimits the somewhat flattish base. The aperture is quadrangular and has a short, twisted anterior canal.

Dimensions. Holotype, BM(NH) GG 5612.

Height (15 whorls)	11·3 mm
Spiral angle	16°
Penultimate whorl height (between sutures) . .	1·2 mm
Penultimate whorl diameter	3·0 mm

Discussion. This species is distinguished from the Lower Aptian *N. subattenuatum* (d'Orbigny) by the absence of an adapical astragal, and from *N. davoustiana* (Cotteau) in the lack of a median tuberculate spiral cord.

Nerineopsis aculeatum (Sharman & Newton), 1896
(Pl. 1, figs 5–8)

1896 *Cerithium aculeatum* Forbes MS, Sharman and Newton: 250.
1961 *'Cerithium' aculeatum* Forbes: Casey: 608.

Lectotype. BM(NH) G 55222 designated here.

Paralectotypes. BM(NH) G 55191–55192; G 55218 & 55219 on the same specimen; G 55220; and G 55223–55228. All these specimens are from the G. W. Lamplugh collection, Speeton Clay, zones C 6–8, Hauterivian. Speeton, Yorks.

Other material. All from the Speeton Clay, Speeton, York. BM(NH) 64121 (3 specimens); 64144 (2 specimens) and 64155, purchased from Lady Hastings, 1855; BM(NH) GG 20789, C. W. Wright collection; Geological Survey Museum 93749.

Description. Small, turreted shell with two strong carinae. Narrow, linear suture, slightly grooved.

The adapical carina, with a strong spiral cord, occurs below the posterior suture and gives rise to a small concave shoulder. The second carina is situated in the centre of the whorl, while there is a third, weaker, carina towards the abapical suture, which tends to mark the periphery of a flat, very slightly convex base. The interspaces between the carinae are occupied by weaker secondary spiral cords; two to three between the adapical and median carinae and one between the median and abapical carinae. The base is ornamented by smooth spiral cords that vary in number and extend on to the columella.

Axial ribs begin at the adapical suture, but, in most cases (e.g. G 55192), these only reach the second, or third spiral cord. The tubercles that develop at the junctions of ribs and cords, contribute to the frilled appearance of the adapical carina. Sometimes the ribs persist and result in a reticulate ornament (e.g. G 55223). It was only possible to count the ribs on two specimens; G 55220 with 24 per whorl and one of the specimens numbered 64144 has 21 per whorl. These so-called 'ribs' (see Sharman & Newton) tend to follow the opisthocline growth lines and it is virtually these growth lines that cause the frilling of the adapical carina. The aperture is seldom preserved sufficiently for adequate description, but would appear to be sub-circular with a short, curved anterior canal.

The variability of ornament in specimens of *N. aculeatum* is quite noticeable, principally occurring in the differing number and arrangement of the weaker spiral cords, but occasionally in the position of the stronger cords and consequently the carinae. In particular, BM(NH) GG 55220 has a strong median carina, whereas the carinae are of equal strength.

Discussion. Although the name *Cerithium aculeatum* was used by Judd (1868: 235, 242) and Lamplugh (1889 : 598) the species was not described or figured by either author, and therefore these references must be considered as *nomina nuda*. Sharman and Newton (1896) were the first to provide an adequate description of this species. However, it was not figured, for their principal concern was to provide an account of a mould found in drift material at Moreseat, near Aberdeen, and which they considered to be a variety of *C. aculeatum*. The specific name has, in the past, been attributed to Forbes, because he attached the name to specimens found in the Speeton Clay.

Sharman and Newton (1896 : 248) mention their consultation with Lamplugh and the fact that they were able to compare the Moreseat mould with his large series of Speeton fossils. It is on this evidence that the Lamplugh material in the BM(NH) collections has been considered as a type series. It was difficult to select a lectotype, since these specimens are either incomplete, or poorly preserved. The best specimen consists only of the earlier whorls, and these do not show the full ornament development.

It should be pointed out that the record of the use of the name *Cerithium aculeatum* (Gmelin) given by Oken (1815 *Lehrbuch Nat.*, iii, 1 : 268) refers to a Recent species, *Potamides* (*Tympanotonus*) *radula* (Linn.) see Tryon (1887, Vol. **9**,: 159), which Gmelin (1790 in the 13th edition of *Linn. Syst. Nat.* : 3523) recorded as *Strombus*. The International Commission of Zoological Nomenclature have decided to place Oken's book on the list of rejected works (Opinion 417, 1956).

The turreted form of *N. aculeatum* (Gmelin) together with the presence of three carinae, of which two virtually form a bicarinate keel towards the base of the whorl, easily distinguish it from the nerineiform *N. attenuatum* (Forbes) with only adapical and abapical carinae. *Cerithium gottfriedi* Wollemann (1900 : 168, pl. 8, fig. 7) from the Neocomian of Brunswick, Germany, has strongly similar ornament to *N. aculeatum*, but can be separated by the presence of projecting thorn-like tubercles on the uppermost spiral cord, its weak mid-whorl spirals and the much weaker development of axial ribbing.

Nerineopsis subattenuatum (d'Orbigny), 1850

(Pl. 1, figs 9 & 12)

1845 *Cerithium attenuatum* Forbes: 352, pl. 4, fig. 11.
1850 *Cerithium subattenuatum* d'Orbigny: 116.

DIAGNOSIS. *Nerineopsis* with adapical and abapical beaded astragals with five to seven spiral cords between them; suture grooved.

MATERIAL. Holotype, in Geological Survey Museum, ex-Geological Society collection, No. 2274, from the Lower Greensand, Atherfield, Isle of Wight. Other material includes Geol. Survey Museum no. 93687 and possibly BM(NH) GG 5610, both from the Crackers Bed, Lower Aptian, Atherfield, Isle of Wight.

DESCRIPTION. Small, slender, nerineiform shell with a slightly concave whorl outline. The suture lies in a furrow formed by the astragals on the adjacent whorls. The width of this furrow is equal to half the height of the whorl. The whorl is ornamented by two similar and faintly beaded astragals, one near each suture, with the spaces between their beads almost equal to the width of a bead. These astragals are separated by a wide area, that is three to four times the width of an astragal, and which is ornamented by a small number of spiral cords that are not clearly preserved in either specimen. The base has a carinate border and a convex surface crossed by spiral threads. The aperture is not preserved in any specimen, nor is there any indication of the growth lines.

Dimensions. GSM 93687.

Height		18·0 mm
Spiral angle	approx.	14°
Penultimate whorl height		1·6 mm
Penultimate whorl diameter		3·7 mm

Discussion. While attempting to identify these Crackers specimens, it was recognised that they have some affinity with Forbes' figure of *Cerithium attenuatum*. On investigating his specimen, (a very poor external impression preserved in a matrix of sandy-clay), the style of ornament confirmed this opinion. It is therefore possible to give a slightly more satisfactory description of this fossil and to point out that the central rib forming a sharp and prominent keel, which he described, is in fact formed by one of the astragals and that the lack of any indication of a suture on the specimen led him astray.

D'Orbigny (1850 : 72 & 116) introduced the name *C. subattenuatum* to replace *C. attenuatum* Forbes, after he had included the Wealden fossil, *Melanopsis attenuatum* J. de C. Sowerby (1836 in Fitton, pl. 22) in the genus *Cerithium*. This rendered *C. attenuatum* Forbes a secondary homonym (see Article 57 and 59b) and although *Melanopsis attenuatum* would now appear to be a Cassiope, or a closely-related form, Forbes' specific name cannot be restored (see Article 57c, Int. Code of Zool. Nomen), as the name had been rejected before 1960.

D'Orbigny's species is similar to *Nerineopsis davoustiana* (Cotteau), 1854 in shell and whorl shape, but in *davoustiana* the abapical astragal is smooth, while *N. subattenuatum* has markedly grooved sutures and a more concave whorl outline. *Cerithium frickei* Wollemann (1906 : 292, pl. 10, fig. 5) is thought to have a more prominent tuberculate abapical spiral cord, but it is impossible to make any further comparison from Wollemann's figure.

Nerineopsis coxi sp. nov.

(Pl. 1, figs 10 & 11)

Diagnosis. Slender turriculate shell, ornamented by three strongly tuberculate spiral cords of which the abapical row is the most prominent.

Holotype. BM(NH) GG 6475, Gault, Folkestone, Kent.

Paratypes. BM(NH) GG 6474, G 73787, G 7411, G 4363 (24 specimens), Middle to Upper Albian, Gault, Folkestone, J. S. Gardner collection; BM(NH) 41731 (3 specimens); and GG 20786–20788, Albian, Lower Gault, Bed 1 (vii), East Cliff, Folkestone, collected by Messrs N. J. Morris, J. D. Taylor and R. J. Cleevely.

Description. A small, slender, turriculate shell, with a finely-channelled suture. The whorl outline is a little concave on either side of a subcentral carina. A protoconch is not available, but the first preserved whorl is smooth and convex, while a smooth spiral cord appears on the second whorl, this is followed by another spiral cord adapical to the first giving the third whorl a bicarinate outline. The opisthocline growth lines then become apparent and it is also possible to discern a further smooth spiral cord at the abapical suture. At the sixth preserved whorl, the adapical cord becomes a line of tubercles, while the appearance of small axial ribs accentuates the growth lines. The ribs extend from the adapical suture to the abapical cord and enlarge these tubercles. At the 'seventh' whorl, tubercles also appear on the abapical cord and this gradually becomes the strongest and subcarinate. At this stage, the tubercles on this cord are quite strong, isolated and projecting slightly abapically. They, later, tend to merge into the cord, which nevertheless persists, giving rise to a carina that is only disturbed by small notches.

On the 'tenth' whorl, a fourth spiral cord develops close to the adapical suture, this soon becomes beaded and, in turn, becomes tuberculate. The number of tubercles per whorl on the stronger abapical carinate cord is about 12–14; on the adapical cord about 16–18 and on the fourth cord about 14–16.

On later whorls, a band of three closely spaced spiral threads occurs midway between the first-formed cords. The flat base is bordered by the third spiral cord described above. A slight spiral occurs at a short distance from the edge and faint traces of flexuous growth lines occur. The aperture is not completely preserved in any of the specimens, but a short, slightly curved, anterior canal is present.

DIMENSIONS. BM(NH) G 73787.

Height (15 whorls)	12·0 mm
Spire angle	12°
Last whorl height	1·5 mm
Last whorl diameter	3·5 mm

DISCUSSION. The distinctive ornament of this species separates it from all other described forms. The slightly sub-central carina, produced by its strongly tuberculate initial spiral cord, easily enables *N. coxi* to be distinguished from forms that have a concave whorl outline, e.g. *N. loryi* (Pictet & Campiche, 1862) and *N. subattenuatum* (d'Orbigny 1850). The three rows of tubercles also serve to differentiate the species from both *N. loryi*, which only has two rows of tubercles (or beads), between its adapical and abapical astragals; and also *C. rochati* Pictet & Renevier, 1854, which also has three tuberculate rows, but in different positions. Although *N. gottfriedi* (Wollemann, 1900) has a row of frilled tubercles, these are close to the adapical suture rather than central. The numerous additional spiral cords of *N. aculeatum* prevent any comparison with *N. coxi*, on account of its slightly frilled adapical carina. Cossmann (1906 : 35) included *Cerithium excavatum* Brongniart, 1822 in his list of *Nerineopsis*, yet without examining actual specimens it is not possible to offer any worthwhile comment on that species. Its concave whorl shape and ornament of a smooth abapical astragal and tuberculate adapical cord would appear to be reasonable features upon which to distinguish this Albian fossil from *N. coxi*.

Nerineopsis melburiensis sp. nov.

(Pl. 1, figs 1 & 2)

DIAGNOSIS. Large *Nerineopsis* with only faint abapical and adapical astragals and fine spiral cords; suture slightly grooved.

Holotype. GSM 93752, the only known specimen.

Locality and horizon. Chloritic Marl, Lower Cenomanian, Melbury Park, nr. Shaftesbury, Dorset.

Description. Nerineiform shell of medium size. The whorl outline is feebly concave with narrow convex margins. The linear suture lies in a furrow bordered by the astragals of adjacent whorls. The width of the furrow is equal to about one-fifth to one-quarter of the height of the whorl. The whole surface, including the two astragals, is crossed by about 20 or more spiral threads, which are separated by interspaces equal to their own width. These threads are unequal in strength and show collabral rugae at intervals.

The base has a rounded edge, within which the surface is convex and crossed by growth-lines and spiral threads. The aperture is small and rhomboidal with an outer lip that has a parasigmoidal outline. The columella is smooth and short. The growth-lines show a moderately deep sinus.

Dimensions. Holotype (GSM 93752)

Height (incomplete 6 whorls)	20·0 mm
Spire angle	11°
Penultimate whorl height (between sutures) . .	3·5 mm
Penultimate whorl diameter	3·6 mm

Discussion. This single specimen differs from other known species of *Nerineopsis* principally in its larger size, but also in the smoothness of its astragals and in the greater number of spirals between them. On comparison with the other large Upper Cretaceous forms assigned to *Nerineopsis* in this paper, it is more elongate and slender than either *N. cuckhamsliensis* or *N. adeli*, while its two astragals appear to be stronger than those of the former.

Nerineopsis cuckhamsliensis (Woods)

(Pl. 1, figs 3 & 4)

1896 *Cerithium cuckhamsliense* Woods: 92, pl. 4, fig. 11.

Holotype. Sedgwick Museum B 4443, from the Chalk Rock of Cuckhamsley, Wilts.

Other material. The only other specimens available are from the Chalk Rock, Holaster planus zone, Turonian, of Hill End, Hitchin, Herts. (BM(NH)G 48978) and Marlow, Bucks. (BM(NH) GG 6286). Woods (1896) also records material from Luton, Beds.

Description. A medium-sized conical shell in which the flat whorl outline is slightly concave before a low abapical carina. The suture is linear and grooved. This groove is bounded posteriorly by the low abapical carina and anteriorly by a rounded, less prominent, adapical shoulder, which gives rise to the slightly pagodiform outline. The apical whorls are not preserved.

Very faint spiral stiare are just visible on some whorls. The aperture and base are imperfectly preserved on the material studied.

DIMENSIONS.

	Holotype SM B 4443	BM(NH) G 48978
Height	approx. 33·0 mm	approx. 26·0 mm
Spiral angle	19·5°	20°
Penultimate whorl height (between sutures)	3·5 mm	3·9 mm
Penultimate whorl diameter	approx. 9·0 mm	9·4 mm

DISCUSSION. This species can be attributed to the genus *Nerineopsis* as its shell form, whorl outline and ornament resemble typical members of that genus.

The slender shape of *N. melburiensis* would appear to separate that species from *N. cuckhamsliensis* and this difference is emphasized by the presence of both adapical and abapical astragals in the former. The strong spiral cords of the Campanian, *N. adeli* are in complete contrast to the very faint spiral threads that can just be distinguished on the poorly preserved examples of *cuckhamsliensis*, while the faintly tuberculate adapical astragal of *N. adeli* is quite distinct from the rounded shoulder present in Wood's species.

Nerineopsis adeli sp. nov.

(Pl. 1, fig. 14)

DIAGNOSIS. Large *Nerineopsis* with grooved suture, adapical tuberculate astragal and nearly smooth abapical astragal separated by six spiral cords.

HOLOTYPE. Unqiue specimen in the Geological Survey Museum, registered number 93753, the only specimen seen.

LOCALITY AND HORIZON. Upper Chalk, ? Campanian, Springbank, nr. Coagh, Co. Derry, Northern Ireland.

DESCRIPTION. The shell is of medium size and cylindrical. The whorl is low and its outline rather flat, or feebly convex. The suture occurs in a furrow bordered by the astragals of adjacent whorls and is of the same width as a primary spiral. There are two astragals, of which the posterior has faint tubercles that are separated by spaces equal to twice the tubercular width, while the anterior astragal is almost smooth. Both the astragals are double the width of a spiral cord and nearly equal to one another. The six spiral cords are separated by very narrow and unequal interspaces of half to one-third their width. The base has a rounded edge and a convex surface crossed by growth rugae and spiral threads. Small, rhomboid, aperture with an anteriorly protruding outer lip. Growth lines show a shallow sinus. Columella smooth.

DIMENSIONS. Holotype (GSM 93753)

Height (6 whorls)	28 mm
Spire angle	20°
Spire whorl height (between sutures)	4 mm
Spire whorl diameter	11 mm

Discussion. The prominent ornament of this species, i.e. the strength of its six spiral cords, the slightly tuberculate appearance of the adapical astragal and its convex whorl outline, easily separate *N. adeli* from either of the other large Upper Cretaceous species described above.

Genus *CIRSOCERITHIUM* Cossmann, 1906

Type species by original designation, *Cerithium subspinosum* d'Orbigny, 1843 = *Cerithium subspinosum* Deshayes, 1842.

Diagnosis. Small shells, of squat conical form, with strongly convex and sometimes angular whorls, forming a rather tier-like spire. The sutures are bordered by a spiral cord that is often granulose. Ornament consists of numerous spiral cords and a smaller number of axial ribs. Tubercles (or nodes) occur at the intersections, particularly on the upper part of the whorl and at the adapical shoulder. Last whorl relatively large, sometimes almost two-fifths of the total whorl height and it has a slight angularity at the base. Base feebly convex and ornamented by numerous spiral threads. Rounded aperture, not sinuous, and a short straight beak at its tip. Outer lip thickened with a strong external varix but this does not have internal lamellae. Columella strongly perpendicular. Parietal lip very straight and a little thickened. Partially, formed anterior canal.

Remarks. Cossmann (1906) only compared his new genus with the similarly ornamented Tertiary *Hemicerithium* Cossmann, 1893. He distinguished them by apertural characters and pointed out that *Hemicerithium* has a definite, short, truncated canal and a visibly twisted columella, while *Cirsocerithium* has a simple beak and a columella that is not twisted at its anterior end, or modified by the beak. It is difficult to fully understand his finer points of distinction, even after a thorough comparison of the figures that he gave for both genera.

Cossmann also referred to the similarity of the columella and beak of *Cirsocerithium* and *Paracerithium* Cossmann, 1902, but separated them by using the columellar characters mentioned above. Such a distinction is also difficult to comprehend for in that feature they appear to be practically identical. However, the apertural varix present in *Cirsocerithium* and their different ornament provide sufficient criteria for distinguishing the two genera.

Nagao (1934 : 253) when describing *Cirsocerithium reticulatum* from the Aptian, Hiraiga Sandstone of Japan, stated that he regarded *Cirsocerithium* as a subgenus of *Cerithium*, but did not proceed to elaborate on his reasons. Presumably, his opinion is based on the interpretation of the short anterior canal, which he evidently considered was sufficiently 'cerithium-like' to warrant closer affinity with *Cerithium*. On the other hand, Cossmann regarded the canal as being rudimentary and therefore included the genus in the Procerithiidae.

Two of the British examples described here can only be tentatively referred to *Cirsocerithium* on the basis of common apertural and ornamental features. The prominent axial ribs of ?*Cirsocerithium kirkaldyi* sp. nov. are very like those occurring in the related genus *Paracerithium*, which is virtually confined to the Jurassic, for the inclusion of the Neocomian species *C. gauthieri* Peron, 1899 in *Paracerithium* is extremely doubtful.

Cossmann's inclusion of the Cenomanian species *C. peroni* Cossmann, 1906 in *Cirsocerithium*, has prompted my decision to provisionally include ?*C. nooryi* sp. nov. in the same genus. Both species have a wide spiral angle producing broad shells, and possess a rounded aperture with an apertural varix, although their general ornament and whorl shapes are quite different.

Cirsocerithium subspinosum (Deshayes), 1842

(Pl. 2, figs 1 & 2)

1842 *Cerithium subspinosum* Deshayes in Leymerie: 14, pl. 17, fig. 12.
1843 *Cerithium subspinosum* Deshayes; d'Orbigny: 364, pl. 229, figs. 4–6.
1903 *Cerithium subspinosum* Deshayes; Wollemann: 32, pl. 4, fig. 11 & 11a.
1906 *Cerithium subspinosum* Deshayes; Wollemann: 290, pl. 10, figs 2–3.
1906 *Cirsocerithium subspinosum* (d'Orb.) Cossmann: 51, pl. 7, figs 1–3.
1949 *Cerithium subspinosum* Deshayes; Collignon: 36, pl. 4, figs 14 & 15.

MATERIAL. Sedgwick Museum, B 32530 and BM(NH) GG 20746.

LOCALITY AND HORIZON. The Gault, Middle or Upper Albian, Folkestone, Kent; also recorded from Albian, Algermissen, Germany (fide Wollemann); Albian, Ervy and Gerodot, Dept. of Aube, France (fide d'Orbigny); Albian, Ambarimaninga, Madagascar (fide Collignon).

DESCRIPTION. Small, subfusiform shell with a convex whorl outline and subsutural ramp. Except for the apical whorls, the suture is linear and grooved.

The first whorl is very small but the whorl size expands rapidly until the fourth whorl, the spiral angle for these initial whorls being approximately 75°. The first and second whorls are rounded and smooth. The third and fourth are angular, having a wide sutural ramp and a flat whorl side that is parallel to the axis but turns in again towards the axis at a second angularity just above the suture. (N.B. This description of the early whorls is based on GG 20746).

On the fifth whorl strong spiral cords have developed along the angularities. These cords are crossed by marked rugae which follow the growth lines. The rugae are strongly opisthocyrt, or slightly opisthocline and are raised as they cross the adapical cord at the edge of the ramp. The sixth whorl has the typical ornament pattern of later whorls, with nine axial ridges per whorl. The axial ridges are tuberculate at the edge of the ramp and gradually taper abapically down the whorl side. Further spiral cords appear in the following positions: a third spiral is introduced on the seventh whorl between the ramp and the cord on the abapical angularity, while another develops on the eighth whorl. On the ninth, the final whorl, intermediate spirals appear between these, and a single cord on the ramp. A series of one strong and four fine spiral cords are present on the base below the abapical angularity.

DIMENSIONS.	SM B 32530	BM(NH) GG 20746
Height	8·0 mm approx.	6·0 mm
Penultimate whorl height	1·5 mm	1·1 mm
Penultimate whorl diameter	3·3 mm	2·2 mm

Discussion. The specimen in the Sedgwick Museum B 32530 (see pl. 2, fig. 1) closely resembles the illustration of Deshayes' holotype and other subsequently figured material. Specimen BM(NH) GG 20746 (pl. 2, fig. 2) differs slightly from these typical forms, in which the axial ridges nearly disappear on the body whorl, by having fewer spiral cords and rather more prominent axial ridges. In many respects, this more acutely-whorled form resembles *Cirsocerithium harborti* (Wollemann, 1908 : 179, pl. 13, figs 5–7) from the 'Upper Neocomian'' but at present, it is considered to be a morphological variant of *C. subspinosum*.

? ***Cirsocerithium kirkaldyi*** sp. nov.

(Pl. 2, fig. 8)

Diagnosis. A possible *Cirsocerithium* ornamented by high, sharply angular, axial ridges on the whorl side and possessing a distinct sutural ramp; the subsutural spiral cord lacks beaded ornament.

Holotype. BM(NH), GG 5603.

Material. The holotype and a single paratype BM(NH) GG 5604 originally in the C. W. Wright collection. Both shells are worn.

Locality and horizon. Ferruginous Sands, Lower Greensand, ? Nutfieldensis Zone, Aptian, Shanklin, Isle of Wight.

Description. A small subfusiform shell with a short spire. The convex whorls have a distinct sutural ramp and are separated by an undulating suture. The material studied lacks the apical whorls. The ornament of later whorls consists of eleven orthocline axial ridges per whorl, and these are separated by interspaces equal to their own width. The axials are slightly flattened in the middle, particularly at the edge of the ramp. On the paratype, there is an indefinite subsutural spiral cord and a further five primary spiral cords, the first being at the edge of the ramp and the fifth at the edge of the base. There are six to seven fine secondary spiral cords on the ramp, three between the first primary (at the edge of the ramp) and the next abapically, and one in each of the remaining interspaces. The base is ornamented by three fine spiral cords and an astragal occurs towards the columella. The latter is crossed by the ends of the axial ridges.

The available material does not show a well-preserved aperture and it is therefore impossible to determine whether or not an apertural varix is present. The growth lines are orthocline on the whorl side, but prosocline on the ramp and apparently prosocline on the base; these presumably represent a sinuously prosocline outer lip to the aperture, a feature which is not typical of *Cirsocerithium*.

Dimensions. Holotype BM(NH) GG 5603

Height	approx.	10·5 mm
Spiral angle		27°
Height of last whorl		6·5 mm
Penultimate whorl diameter		5·5 mm

Discussion. Although lacking the characteristic apertural varix of the genus and possibly having a sinuous outer lip, the remaining features of this species suggest an affinity with *Cirsocerithium*. ?*C. kirkaldyi* differs from both the type species *C. subspinosum* and *C. harborti* (Wollemann, 1908 : 179, pl. 13, figs 5–7), by not having beaded ornament on the subsutural spiral cord. In this way it resembles *C. aptiense* (d'Orbigny 1843 : 363–364, pl. 229, figs 1–3). It differs from all three species in having more prominent axials, particularly at the edges of the ramp. This ramp also appears to be flatter at approximately 45° to the axis, when compared with *C. aptiense* (40°) as figured by d'Orbigny. A further difference is that the edge of the ramp is relatively closer to the adapical suture in ?*C. kirkaldyi* than in *C. aptiense*.

Finally, the resemblance of ?*C. kirkaldyi* to the Jurassic genus *Paracerithium* in possessing very strong axial ribs and an adapical ramp, is repeated.

? ***Cirsocerithium nooryi*** sp. nov.

(Pl. 2, figs 3 & 4)

Diagnosis. Conical littoriniform species with beaded spiral cords but no axial ridges and bearing an apertural varix.

Holotype. BM(NH) 98208. This unique shell is replaced by limonite and is slightly crushed.

Locality and horizon. Lower Chalk, Cenomanian, Ditchling, Sussex.

Description. Small to medium-sized shell, rather large for genus. Conical to littoriniform with a rounded periphery. Whorl outline slightly convex with a grooved suture. Aperture, broad, oval and oblique; outer lip has a shallow sinus and a rounded apertural varix; both inner and outer lips are smooth and reflected outwards.

Ornament consists of granulose (beaded) spiral cords. The initial whorls show four beaded primary spiral cords separated by interspaces nearly equal to their own width. Beads on successive spirals follow the opisthocyrt growth-line direction (i.e. they are slightly curved). On later whorls secondary beaded spirals appear and on the body whorl these may become as prominent as the primary cords. The adapical spiral cord is separated from the rest of the spirals by a slightly wider interspace. It forms a partial shoulder on which the preceding whorl rests. The convex base is not delimited from the whorl side and is crossed by almost smooth alternating primary and secondary spirals.

Dimensions. Holotype BM(NH) 98208

Height . . .	25 mm
Spiral angle . . .	32°
Penultimate whorl height (between sutures) . .	4 mm
Penultimate whorl diameter . . .	9 mm

Discussion. This species is provisionally included in the genus *Cirsocerithium* principally on the basis of its rounded aperture and apertural varix, the opisthocyrt growth lines and the presence of a strong adapical subsutural spiral cord. Its broad shell and wide spiral angle resembles another Cenomanian species, *C. peroni* Cossmann

1906, which Cossmann included in his description of the genus. However, these two species differ in their general whorl shape and ornament. The weak development of the axial ornament, the flattish whorl sides, a smaller number of spirals and its rounded shell-shape immediately distinguish it from the type species *C. subspinosum* Deshayes.

Genus ***NUDIVAGUS*** Wade, 1917

Type species by original designation, *Nudivagus simplicus* Wade, 1917.

Diagnosis. (after Sohl, 1960 : 79). Large turriculate shell, with numerous smooth, flat-sided whorls forming an evenly tapering spire; sutures deeply impressed; growth lines prosocline; aperture sub-ovate to sub-rhomboidal, anterior canal short and slightly curved, inner lip smooth, lightly callused columellar lip.

Discussion. Sohl (1960) pointed out that the sub-ovate apertural outline, short curved anterior canal and the lack of a thick parietal wall callus, serve to distinguish the fusiform *Nudivagus* from *Gymnocerithium* Cossmann, but ally it to the Procerithiidae. Wade (1917) has shown that apertural and columellar features separate *Nudivagus* from other Cerithiacea which have some similarity in shape, e.g. *Clava* and *Cerithium*.

Nudivagus morrisi sp. nov.

(Pl. 2, figs 11 & 12)

Diagnosis. *Nudivagus* with axial ribs occurring on all whorls, an angular basal edge and opisthocyrt growth lines.

Material and occurrence. Geological Survey Museum 2252, an external mould from the Ferruginous Sands, (? Group XIV), Aptian, Nutfieldensis Zone, Shanklin, Isle of Wight.

Description. Medium-sized shell with an elongate fusiform spire. Whorl outline flat, or feebly convex. Simple impressed suture. The rounded earlier whorls show a large number of orthocline to opisthocyrt axial ribs. Ornament of later whorls consists of numerous very fine spiral threads that are crossed by equally fine opisthocyrt growth lines. The base of the whorl is slightly convex and has an angular margin. The aperture is incomplete, but would appear to be prolonged anteriorly into a short beak.

Discussion. The whorl shape, impressed suture and relatively smooth shell with its ornament of fine spiral threads and growth lines, are very similar to the features of *Nudivagus simplicus* Wade (1917 : 297, pl. 19, figs 4 & 5) from the Upper Cretaceous Maastrichtian, Ripley Formation of Texas, U.S.A. It would appear to differ from that species, in having axial ribs on the rounded early whorls, a much sharper basal edge and opisthocyrt, rather than prosocline, growth lines. The strongly convex whorl outline of another American Maastrichtian species, *Nudivagus ?cooperensis* Stephenson, (1941, pl. 54, figs 11 & 12) precludes any comparison. *Cerithium* (*Fibula*?) *detectum* Stoliczka (1868 : 192, pl. 15, fig. 1), a species with strongly rounded whorls, and originally included in *Nudivagus* by Wade, would seem to require further investigation before it can be accepted as belonging to the genus.

At first sight, Casey's Cretaceous genus *Brightonella* appears to have some general similarity with *N. morrisi*, but on examining the holotype of *B. sandlingensis* Casey (1961 : 591) it was possible to note several differences. *N. morrisi* has a much wider spiral angle, its growth lines are more chevron-like and the last whorl has a slight sub-sutural ramp that is not present in *Brightonella*. The holotype of *B. turris* Casey, the type species of the genus, a rather crushed specimen, and other examples in the collection of the Geological Survey Museum, appear to support these differences. The short anterior canal present in *Nudivagus* serves to distinguish it from the Pseudomelanidae, the family to which *Brightonella* has been assigned.

Genus ***BATHRASPIRA*** Cossmann 1906

Type species by original designation, *Bathraspira tecta* (d'Orbigny) 1842.

REMARKS. A number of authors have described new species since Cossmann erected this genus in 1906, with the result that this group is another in need of considerable revision. Unfortunately, no useful investigation can be undertaken with the very few specimens available, due, in part, to the lack of precise stratigraphical information. In order to assess the variation in both ornament and shape, interpret the species, to then decide the number of species present at a particular horizon, and ultimately to infer their phylogenetic relationships, it is necessary to obtain further well-localized material and to re-examine type material. Therefore, for the present, I have only attempted to describe the specimens present in museum collections in Britain and consider this to be a preliminary to the more detailed investigation of the genus. Regrettably this has led to the description of new species from single specimens. Existing British material is the result of meticulous collecting by and on behalf of J. S. Gardner in the past, and more recently by Mr C. W. Wright.

Despite the qualifications expressed above, it is possible to observe that there is a general tendency for ornament to increase in this genus of Cretaceous gastropods, progressing from the Aptian *B. shanklinensis* to the strongly ornamented Albian *B. brightoni*.

Finally, it should be mentioned that the lack of suitable material has prevented redescription of the species *B. neocomiensis* (d'Orbigny) 1843.

Bathraspira tecta (d'Orbigny), 1842

(Pl. 3, fig. 1)

1842 *Cerithium tectum* d'Orbigny: 368, pl. 230, figs 4–6.
1862 *Cerithium tectum* d'Orb.; Pictet & Campiche: 295, pl. 71, fig. 12 and p. 303.
1903 *Cerithium tectum* d'Orb.; Wollemann: 31, pl. 4, fig. 10.
1906 *Cerithium tectum* d'Orb.; Wollemann: 289, pl. 9, figs 8 & 9.
1906 *Bathraspira tecta* (d'Orbigny) Cossmann: 53, pl. 6, figs. 25–27.
1908 *Cerithium* (*Bathraspira*) *tectum* (d'Orbigny) Wollemann: 192.
1948 *Mesalia* (*Bathraspira*) *tecta* (d'Orbigny) Delpey: 18, pl. 4, figs 3–4.
1961 *Mesalia* (*Bathraspira*) *tecta* (d'Orbigny); Casey: 530 and 607.

Material and occurrence. BM(NH) GG 6227, C. W. Wright collection from Lower Albian, Tardefurcata Zone, Regularis sub-zone, Arnold's Pit, Billington Crossing, Leighton Buzzard, Beds. BM(NH) GG 20790, Albian, Gault, Folkestone, Kent.

Discussion. *Bathraspira tecta* has been described in several of the references given above and it is recorded from the Lower Albian of France, Germany, Switzerland and Madagascar. The only previous British records, apart from Casey's (1961) inclusion of the name in a Lower Cretaceous faunal list (where he records it from the main Mammilatum Bed at Folkestone), are those of Price (1874 and 1879). These references were the basis for the inclusion of *tecta* by Jukes-Browne in his list of Cretaceous molluscs (1900 : 461) where he listed two specimens from the Lower Gault and three from the Upper Gault of Folkestone. Originally, Price (1874) had thought this fossil was found only in Bed 7, but later (1879), he recorded it from his Beds 2, 6 and 7 in the Lower Gault and Bed 9 in the Upper Gault. However, if the BM(NH) specimen GG 6227 is correctly identified, it would provide a slightly older record for Britain than any of these.

Jukes-Browne also listed two specimens of *Cerithium ervynum* d'Orbigny, 1843 from the Lower Gault, but considering the higher horizon from which this species has generally been described, these may also have been *B. tecta*. Forbes (1845 : 351) mentions *tecta* as a variety of *B. neocomiensis* (d'Orb.) 1842, yet his interpretation should probably be disregarded for the specimen he figured (pl. 4, fig. 8) as *neocomiensis* and now in the Geological Survey Museum No. 2272, is thought to be a specimen of *Anchura carinella* (d'Orbigny). Such a conclusion verifies the doubts expressed by Pictet and Campiche (1862 : 298) as to his identification.

D'Orbigny readily distinguished *B. tecta* from all other species by means of its characteristic pagodiform shape, which is the result of the contiguity of the concave adapical part of the whorl and the sharp, posterior carina. However, it must be remembered, that d'Orbigny was referring to the interpretation of the genus *Cerithium* current at that time, a group which virtually included all taxa now placed in the superfamily Cerithiacea. The specific features that d'Orbigny mentioned, including opisthocline growth lines, fine spiral ornament and a second, less prominent carina, are apparent in the majority of the figures published to illustrate the species. Wollemann (1906 : 289) also mentions the gradual disappearance with age of the fine spiral cords on the adapical parts of the whorl. D'Orbigny figures a third prominent cord below the bicarinate keel of the body whorl.

GG 6227 (Pl. 3, fig. 1) fits these descriptions exactly; its fine spiral cords appear to alternate in strength and are evenly spaced, while there is a strong indication of a third prominent cord on the base of the body whorl. Unfortunately, the aperture is not visible, although it is obvious (Text-fig. 1) that a short anterior canal is present.

Another probable specimen of *B. tecta*, GG 20790, has two interesting features. Firstly, its posterior carina has a slight tendency to become accentuated adapically and this is reminiscent of *B. cleevelyi* and *B. shanklinensis* (see p. 127). Secondly, the thickening of the two median spiral cords may also reflect a connection with *B. cleevelyi*, which has a single median carina.

Pictet & Campiche (1862) compared *B. tecta* with *Cerithium gurgitus* Pictet & Roux (1849 : 280), yet, although all their specimens were internal moulds, they considered that the species were easily separated on account of their differing spiral angles (quoted as 37° or more for *tecta* and up to 27° for *C. gurgitus*), while the latter was also considered to be more elongate.

In addition to their different stratigraphical occurrence, *B. tecta* and *B. neocomiensis* (d'Orbigny) 1843, can be separated by their slightly different spiral angles, although a comparison of their prominent carinae provides the easiest method of distinguishing them. *B. tecta* normally has two strong carinae, while *B. neocomiensis* has three, the first close to the suture, a strong central one and a third, which is far stronger than the third cord seen on the body whorl of *B. tecta*.

Similarly, although it would seem that *B. tecta* occurs at a lower horizon than *B. fouadi* (Upper Albian), the two species can also be separated by ornamental differ-

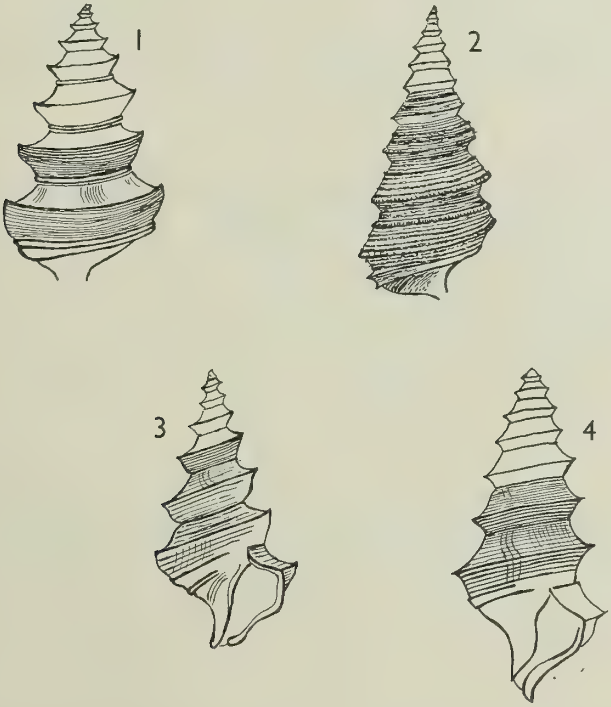

FIG. 1. 1, *Bathraspira cleevelyi* sp. nov., Albian, Locality uncertain (see text). BM(NH). GG 5607. ×2·5. 2. *Bathraspira fouadi* sp. nov., Upper Albian, Folkestone, Kent. BM(NH). G 73795. ×5. 3 & 4, *Bathraspira tecta* (d'Orbigny); Fig. 3, Sketch from d'Orbigny's original figure (pl. 238, fig. 4); note suggestion of a third carina; Fig. 4, (after Wollemann, 1903). ×2.

ences. The former, normally has two carinae and a concave adapical whorl, while in *fouadi* the adapical part of the whorl is straight and relatively elongate and there are three definite carinae (see p. 128).

Peron (1900 : 195), in his comments on the extremely ill-founded Neocomian species *B. beaudouini* (d'Orbigny) 1844, considered that it had a great resemblance to *B. tecta* and could only be distinguished from it by the absence of the pronounced longitudinal striae present in the latter. However, he omitted to make the more justifiable comparison of *B. beaudouini* with *B. neocomiensis*.

Wollemann (1906 : 290) also regarded his Lower Albian species *Cerithium schrammeri* from the Tardefurcataschichten of Algermissen, Germany as being similar to *B. tecta*, but stated that it lacked the constriction below the principal keel. After comparison with his figure, it is difficult to interpret this comment, as the most significant difference would seem to be in the presence of two strong spiral cords on the adapical slope.

Pčhelincev (1927 : 996, 997) has described and badly figured two species, *B. ornata* and *B. multistriata* from the Lower Albian of the Volga Region. Either, or both, of these could be synonymous with *B. tecta* but are said to differ in their sculpture and smaller spiral angles. As justification, Pčhelincev gave the angles as between 35°–40° and he has presumably, taken the figure of 47° given by d'Orbigny rather than the 37° quoted by Pictet and Campiche.

Bathraspira shanklinensis sp. nov.

(Pl. 3, figs 3–6)

DIAGNOSIS. Small pagodiform shell with three strong spiral carinae, the upper edge of the most adapical carina being accentuated and upturned.

MATERIAL. Holotype BM(NH) GG 5602, Ferruginous Sands, Lower Greensand, Upper Aptian, Shanklin, Isle of Wight. Collected C. W. Wright.

PARATYPE. BM(NH) G 20956, Lower Greensand, ?Lower Aptian, Redcliff, Sandown, Isle of Wight.

DESCRIPTION. This small shell has a short, strongly pagodiform spire with a whorl outline that is concave adapically and convex abapically. The suture is linear and moderately deep. The apical whorls are missing in the holotype, but later whorls are ornamented by two spiral carinae of which the posterior is the most prominent. A third carina can be seen on the body whorl and is presumably obscured earlier. The strong posterior carina is practically central on the whorl and the pagodiform appearance of the shell is accentuated by its upper edge becoming upturned to form a sharp ridge. In both specimens, the adapical surface of the whorl is poorly preserved but appears to be virtually smooth, whereas the whole surface below the posterior carina is crossed by equally spaced and prominent, fine spiral threads. The convex base is also ornamented by fine spirals. On the body whorl, growth lines become prominent at unequal intervals. The aperture is not completely preserved, but is roughly pentagonal and a short curved anterior canal is present.

DIMENSIONS. Holotype BM (NH) GG 5602.

Height (4 whorls)	11·7 mm
Spiral angle	20°
Whorl height	7·0 mm
Whorl diameter	7·5 mm

DISCUSSION. The characteristic pagodiform shape and shell ornament establish this fossil as belonging to *Bathraspira*, while the three very strong carinae immediately distinguish it from any other species of that genus. The distinctive upturned edge of the most posterior carina is also seen in *B. cleevelyi* and a specimen of B. *tecta* shows the same feature. This character considered in conjunction with the virtual exclusion of all ornament on the adapical ramp in each of these species, leads to the conjecture that there is some close affinity between them, or that this development may have some ecological significance. *B. excavata* Nagao (1934 : 258, pl. 34, figs 5 & 8) from the Cretaceous, Aptian, Hiraiga Sandstone of Japan, possesses a similar, sharp, upturned ridge on the posterior carina. However, the general whorl shape of this species is more convex and none of the spiral cords are as strong as those of *B. shanklinensis*.

The dramatically upturned carina of *B. shanklinensis* enables it to be distinguished easily from the earlier *B. neocomiensis*. This carina is undoubtedly the strongest of the three present; whereas, in *neocomiensis*, it is the central one that is most prominent.

A. N. Ivanova (1959 : 362, pl. 15, figs 11 & 12) has described an Aptian gastropod from Saratov, U.S.S.R. as *Bathraspira subornata*. Although this is poorly figured, it is possible to discern a median carina, an abapical spiral cord and the concave form of the adapical half of the whorl. The last whorl is said to have a third carina on the base of the shell. In the figure, the fine axial riblets ornamenting the whorls, appear to be tubercles, or at least much stronger than described; and these alone would distinguish that species from *B. shanklinensis*.

Bathraspira cleevelyi sp. nov.

(Pl. 3, fig. 10)

DIAGNOSIS. Pagodiform shell with prominent median, slightly upturned, carina; smooth concave adapical whorl surface, while convex lower whorl ornamented by numerous spiral cords and a smooth astragal towards the base.

MATERIAL AND LOCALITY. BM(NH) GG 5607a & b. Lower Albian, Tardefurcata Zone, a split Regularis-nodule from either Leighton Buzzard, Beds., or Bed 5, Ford Place, Wrotham, Kent.

DESCRIPTION. A small pagodiform shell with whorls that are approximately concave posteriorly and convex anteriorly of a median carina, and which are separated by a finely-channelled suture. The concave adapical part of the whorl is accentuated by a thin upturned carina and, apart from the growth lines, is quite smooth. The outer side of the carina and the abapical part of the whorl are ornamented by a large number of spiral cords (29 are visible on the incomplete body whorl). The cords on the carina are close together, but below this they are more evenly spaced and of equal strength until reaching a strong cord towards the base that forms an astragal. The aperture is not preserved in this unique specimen. Growth lines are opisthocyrt and suggest a shallow apertural sinus at the ramp.

Dimensions. Holotype. BM(NH) GG 5607.

Height (6 whorls)	approx.	18·0 mm
Spiral angle		23°
Penultimate whorl height		4·0 mm
Penultimate whorl diameter		9·3 mm

Discussion. The distinctive strong, rounded cord forming an astragal towards the anterior, and the regularity of its numerous spiral cords serve to distinguish this from other described species of the genus.

Bathraspira fouadi sp. nov.

(Pl. 3, figs 7, 12 & 13)

Diagnosis. Pagodiform shell frequently with three carinae of which the most posterior is the strongest; adapical slope of variable form ranging from straight and elongate to concave and ornamented by numerous, or few spiral cords.

Holotype. BM(NH) G 73795, J. S. Gardner collection.

Paratype material. BM(NH) G 71562, GG 20792–20797; Sedgwick Museum B 32524.

Locality and horizon. All from Folkestone, Kent and probably the Upper Albian.

Description. Small, pagodiform shell with a channelled suture. At least three carinae occur, of which the most posterior is the strongest. Although this prominent carina is in the centre of the whorl, the relatively flat, or concave, adapical slope above it appears to occupy the upper two-thirds of the whorl. In the holotype (G 73795) and paratypes (GG 20794–20795), this is accentuated by the numerous spiral cords ornamenting this slope (see Text-fig. 1).

Ornament consists of spiral cords that are crossed by thin collabral threads. On the initial whorls, this produces a reticulate pattern, but on later whorls (particularly in the elongate varieties) the cords have a beaded appearance. The spaces between the collabral threads are extremely variable and they are frequently three times the width of a thread. The spiral cords vary in number, strength, pattern and position.

Primary and secondary cords alternate on the adapical slope, with the second of the primary cords being fairly prominent (see holotype G 73795. pl 3, fig. 12). Abapically to the dominant carina, the whorl slopes away to a moderate basal carina and this surface is ornamented by a varying number of spiral cords. Occasionally, e.g. GG 20792, one of these cords is strong enough to produce a third carina. In the holotype a small shelf is produced just above the basal keel.

Normally, only a single spiral cord occurs at the prominent carina, but in the holotype there are three, and in G 71562 and SM B 32524 there are also several cords.

A number of fine spirals occur on the convex base and these are crossed by the growth lines. The growth lines show a wide shallow sinus, that has its apex at the principal carination. The aperture is not completely preserved in any specimen, but would appear to be sub-orbicular in shape and to possess a short anterior canal.

DIMENSIONS.

	SM B 32524	Holotype BM(NH) G 73795	BM(NH) GG 20793
Height	approx. 19·0 mm	21·0 mm	14·2 mm
Height of last whorl	approx. 10·0 mm	8·0 mm	5·9 mm
Maximum diameter	9·7 mm	9·6 mm	7·2 mm
Outside spiral angle	31°	27°	29°

DISCUSSION. The specimens included in this species show considerable variation in both ornament and the form of the adapical slope. Some of the most variable forms are figured on pl. 3 and have fewer spiral cords, a more concave adapical slope and several spiral cords on the prominent carina. In G 71562 the carina is much wider than usual, while in S.M. B 32524 it is much sharper. It is possible that G 73797 (see pl. 3, fig. 13)—a specimen in which the adapical ornament is strongly developed and also shows some variation in the position of the abapical keels—might be recognized as another variety, or even with more material a separate species. The ornament and generally straight, elongate form of the adapical slope provide sufficient criteria to distinguish *B. fouadi* from other known species, e.g. *B. tecta*.

B. neocomiensis (d'Orbigny 1843, pl. 232, figs 8–10) also possesses three carinae but the central one is the most prominent and enables the two species to be separated. It may be worth noting that the stronger spiral cord on the adapical slope of *B. fouadi* occurs in a similar position to the posterior carina of *B. neocomiensis*. The smaller spiral angle of *B. fouadi* (31°) assists in separating it from the Lower Albian *B. tecta* (37°). The latter also has an ornamented adapical slope, but this is concave and its spiral cords are not beaded. The variable forms of *fouadi* are in many respects, intermediate between *B. tecta* and the holotype *B. fouadi*.

The strong development of spiral cords in *B. brightoni*, which produce an irregular whorl outline, readily distinguish it from *B. fouadi*. The position of the adapical carina in the former also coincides with that of the stronger spiral cord in *fouadi*. The convex appearance of *B. ervynym* (d'Orbigny, 1843 : 367, pl. 230, figs 1–3) enables it to be distinguished from *B. fouadi*, although the unequally distributed spiral cords, small spiral angle (25°) and the more abapical position of its prominent carina are other useful distinguishing features.

Bathraspira brightoni sp. nov.

(Pl. 3, figs 9 & 14)

DIAGNOSIS. Pagodiform shell, with 2 carinae; whorls ornamented by spiral cords that are strongly developed on the adapical slope, one of which forms an astragal or third carina, giving the whorl an undulating outline.

HOLOTYPE. BM(NH) G 73796, J. S. Gardner Collection, Albian, Gault, Folkestone, Kent.

OTHER MATERIAL. BM(NH) 34843, Albian, Upper Greensand, Blackdown, Devon; BM(NH) GG 20791, Gault, St. Florentin, Yonne, France, may belong to this species.

DESCRIPTION. Medium-sized shell with a channelled suture and its pagodiform shape is emphasized by the strong development of several spiral cords. On the initial whorls two of these produce carinae, with the abapical one the more dominant. Later, a third carina develops abapically to these. The crest of the principal carina is rounded, carrying three to four strong spiral threads. Two similar cords occur on the posterior carina.

The whorl outline is convex between the suture and the adapical carina and ornamented by a weak and a strong spiral cord. Below this, and before the main carina, the whorl is concave. Eleven variable spiral cords of which the fifth and ninth are particularly strong, ornament this surface. Anterior to the rounded main carina, the whorl again becomes concave and is covered by four equally spaced cords. Finally, the surface abapical to this, is covered by a further six spiral cords, with an indefinite number of threads on the convex base and within a slight basal carina.

The spiral cords are crossed by thin collabral threads, that are regular and separated by interspaces equal to twice their width. The growth lines show a shallow U-shaped sinus with its apex lying on the dominant carina. The aperture is not completely preserved, but in GG 20791 part of a short curved anterior canal is present.

DIMENSIONS. Holotype BM(NH) G 73796.

Height (10 whorls)	16·3 mm
Spiral angle	23°
Penultimate whorl height (between sutures) . .	4·2 mm
Penultimate whorl diameter	7·0 mm

DISCUSSION. Despite its poor preservation, the Blackdown BM(NH) 34843 specimen appears to belong to this species. It has a roughly similar whorl shape with virtually identical ornament, but the adapical carina is almost as prominent as the central one. In the slightly flattened French specimen GG 20791, the prominence of the main carina, and the concavity in the whorl outline, are not developed to the same degree as those of the type, but again, ornament is identical, with its strong spiral cords in exactly similar positions.

The characteristic whorl outline consisting of prominent carinae and their intervening sulci separate this species from other Cretaceous members of the genus.

The development of several cords on the carinae can also be observed in specimens of *B. fouadi*. The identical positions of the prominent adapical cord of *B. fouadi* and the adapical astragal of *B. brightoni* are also significant indications of a close relationship.

The record of *Cerithium neocomiensis* by Price (1879 : 67) from the Blackdown Greensand could have been another example of this species.

Genus ***METACERITHIUM*** Cossmann, 1906

TYPE SPECIES. By original designation, Cossmann (1906 : 54), *M. trimonile* (Michelin).

DIAGNOSIS. (After Cossmann, 1906 and Wenz, 1939).

Medium-sized to small, turriculate, conical shell. Sharp spire at summit. Numerous, narrow, flat-sided whorls, that broaden at their base. Ornament generally consists of three granulose spiral cords. Growth lines parasigmoidal. Grooved linear suture. Last whorl not particularly high and angular at basal periphery. Sloping base weakly convex, ornamented by fine spiral cords and strongly curved collabral threads. Aperture sub-rectangular, weakly channelled posteriorly and with a short rudimentary anterior canal. Outer lip strongly sinuous adapically and projecting anteriorly. Columella slightly curved, straight initially but twisted at its anterior end, with an oblique columellar fold. Parietal lip quite thick but not extensive.

REMARKS. Cossmann (1906 : 21) considered that the rudimentary canal of *Metacerithium* had derived from the 'beak' of *Paracerithium*, but he also realized that the fossil evidence indicated that such a feature had evolved independently in different groups at different times. The poor preservation of later Cretaceous material prevented him elaborating on the development from *Metacerithium*, but in this connection, he referred to the occurrence of undoubted members of the Cerithiidae, i.e. with a well-formed prominent anterior canal, in the Turonian.

Cossmann distinguished *Metacerithium* from *Paracerithium* by the protrusion of its rudimentary canal from below the general line of the aperture and shell and referred to it as a 'rudimentary neck'. In association with this, the whorl becomes more convex and, in effect, the aperture widens with the lower lip extending adaxially.

Pčhelincev (1953 : 190) stated that the basic features of ornament in *Metacerithium* have remained stable and that consequently it is extremely difficult to separate specimens from quite different stratigraphical horizons using this character. The British Cretaceous examples of the genus, e.g. *M. trimonile*, show that there is considerable range of ornament within a species, but until more details of its range and development have been obtained, it is not feasible to dismiss Pčhelincev's assertion. However, it is probable that an investigation of the development of the ornament will be significant in understanding the evolution within the genus.

Metacerithium turriculatum (Forbes)

(Pl. 5, figs 8–11)

1845 *Cerithium turriculatum* Forbes: 352, pl. 4, figs 7a & 7b.
1862 *Cerithium turriculatum* Forbes; Pictet & Campiche: 301.
1961 *'Cerithium' turriculatum* Forbes; Casey: 608.

SYNTYPES. Geol. Survey Museum, Geol. Soc. Collection, 2253 and 2255, stated to come from the Lower Greensand, Crackers Bed, Atherfield, Isle of Wight. Although each specimen has been labelled according to the figure with which it is alleged to correspond, there is no exact resemblance between any of the specimens and Forbes' figures. This may be due to the specimens suffering some slight damage, but is more probably a result of the original figures being rather stylized.

OTHER MATERIAL. BM(NH) G 20907, G 70131, G 74602, GG 5640 and GG 20812–20814 all from the Lower Greensand, Atherfield, Isle of Wight. BM(NH) GG 6087 an external mould from the Atherfield Clay, Littleton, nr. Guildford, Surrey; G 20878, Atherfield Clay, Sevenoaks Tunnel, Kent; and Geol. Survey Museum 93681, (Atherfield Clay), East Shalford, Surrey.

HORIZON. Lower Greensand, Lower Aptian, Deshayesites forbesi Zone.

DESCRIPTION. Small turriculate shell, with a tuberculate carina situated one third of the whorl height away from the adapical suture and a virtually smooth beaded (or growth-line notched) spiral cord at the adapical suture. This cord gradually becomes wider giving rise to a slight sutural shelf on later whorls and is emphasized by the slight groove that occurs beneath it. The suture is grooved and moderately deep. On the body whorl a secondary carina occurs below the principal one.

The tubercules are particularly strong on the early whorls and almost equivalent to ribs. Subsequently, they become more noded and concentrated at the carina, although still tapering adapically and abapically (later, this effect is only apparent on the adapical slope). The tubercules gradually increase in number (about 8–10 per whorl at first, to 12–16 later) and have a tendency to become slightly opisthocline on later whorls. In common with other species of *Metacerithium* the tubercles virtually disappear on the body whorl.

The adapical slope is feebly concave, while the abapical one is convex. Their surfaces are almost smooth, but variable development of fine spiral threads and the growth lines can produce a cancellate ornament in some specimens, particularly on the adapical surface. In others, the growth lines are at first opisthocyrt, then become opisthocline below the tuberculate carina and finally swing back to the short, thick columella, i.e. they may be described as parasigmoidal.

The almost smooth convex base is bordered by the slight secondary carina. The aperture appears to be of average size and has a short anterior canal.

DIMENSIONS.

	BM(NH) G 74602	*M. rikuchuense* Nagao (see under discussion)
Height (9 whorls)	11·0 mm	17·0 mm approx.
Spiral angle	15°	15°
Whorl diameter	5·0 mm	6·3 mm
Whorl height	4·2 mm	

DISCUSSION. This species is readily distinguished from other species of *Metacerithium* by the prominent, beaded spiral cord close to the adapical suture. The whorl shape and strong tuberculate carina also provide other diagnostic characters. A similar ornament pattern occurs on the early whorls of *M. trimonile.* In his figures of *M. turriculatum* Forbes appears to have accentuated the tubercles, for they are not quite so strong in the actual specimens and are typically reduced on the last whorls.

Apart from brief records in lists, e.g. Blake (1902 : 15) and Casey (1961 : 608) the species has not been mentioned in the literature since Forbes' original description. Pictet & Campiche (1862 : 301) did comment on the association of a species '*C. tuberculatum* Forbes' by d'Orbigny (1850 : 116) with *C. aptiense* d'Orbigny. They concluded that it was a misprint for *C. turriculatum* Forbes and decided that the dominant carina and larger tubercles of *C. aptiense* were sufficient to distinguish the two.

The ornament shown on the earlier whorls in figures of *C. disparile* Buvignier (1852 : 42, pl. 28, figs 5a & b) is partly comparable to that of *C. turriculatum*. However, any resemblance is limited to the beaded adapical cord and growth line shape, for the carina is not tuberculate and occurs mid-whorl, nor is there any indication of a secondary carina towards the base.

M. turriculatum (Forbes) is obviously closely related to *M. rikuchuense* Nagao (1934 : 256, pl. 35, figs 4–7) from the Aptian, Hiraiga Sandstone of Japan. Nagao's figures are not particularly clear, but the 'supra-sutural band', ornamented by rounded granules, that he describes is identical to the beaded spiral cord occurring in *M. turriculatum*. The whorl shape of the two species appears to differ; that of the Japanese species being three times broader than high, with flatter whorls and a less inflated base. Nagao also describes the opisthocline growth lines as being rib-like and divided into two by a narrow, indistinct, spiral depression.

Metacerithium trimonile (Michelin), 1838

(Pl. 4, figs 2, 3, 7, 8 & 10)

1838 *Cerithium trimonile* Michelin: 100, pl. 12, fig. 5.
1844 *Cerithium trimonile* Michelin; d'Orbigny: 369, pl. 230, figs 7–9.
1845 *Cerithium trimonile* Michelin; Reuss: 42, pl. 60, fig. 2.
1862 *Cerithium trimonile* Michelin; Pictet & Campiche: 303.
1868 *Cerithium trimonile* Michelin: Stoliczka: 199, pl. 15, fig. 9; pl. 19, figs 2 & 3.
1906 *Metacerithium trimonile* (Michelin) Cossmann: 54, pl. 6, figs 29–31.

MATERIAL. BM(NH) J. S. Gardner Collection, GG 6470–6472, GG 20799–20811 and G 73794.

LOCALITY AND HORIZON. Middle to Upper Albian, Gault, Folkestone, Kent. *Metacerithium trimonile* has been recorded from the Albian of both Germany and Switzerland and is common in the Gault of France.

DESCRIPTION. Medium-sized, slightly coeloconoid shell that Stoliczka (1868) has described as awl-shaped. Whorls increase very gradually in height and width, but are three to four times broader than high. Grooved sutures occur 1–2 mm below a basal carina and above the slight bevel at the top of the succeeding whorl; consequently the groove is asymmetric. Each of the later whorls are ornamented by three rows of small rounded tubercles, which are smaller but more numerous on the posterior row, rather weaker on the central row and strongest on the anterior row. Some variation in this pattern is apparent within the material available. Occasionally, the abapical row on the body whorl is merely a carina with breaks caused by the crossing of the growth threads. The number of tubercles per row decreases as their strength increases, e.g. posterior row 15–18 per whorl; centre row 13–15; anterior row 12 per whorl. The entire whorl surface is also covered by faint spiral threads and opisthocline growth lines. The abapical row of tubercles occurs on, or at the basal carina and the smooth convex base is below this. The growth lines (see pl. 4, fig. 3) above this 'carina' are opisthocline, but beneath, they first continue forward to produce a rounded projection on the base and then swing back towards the columella. The aperture is quadrangular and prolonged anteriorly into a short curved canal.

The early whorls have been completely preserved in several specimens and it has been possible to observe the sculptural ontogeny of the shell. In some respects this differs from the description by Stoliczka (1868 : 199). On the second whorl, there are about ten opisthocline axial ribs and by the third whorl these are well-developed. A smooth sub-sutural band becomes apparent above the ribs on the fourth and fifth whorls. The axial ribs gradually thicken and now only number eight per whorl. Eventually this thickening leads to the ribs becoming nodose at their anterior end and on the tenth whorl this produces a carina. At the same time, there is a tendency for them to straighten, i.e. become more orthocline.

Meanwhile on the subsutural band there are indications of nodes, these gradually become tuberculate and the whole band projects a little. By the tenth whorl this results in an established tuberculate carina. On the eleventh whorl, the axial ribs begin to separate into two, giving rise to the central and anterior rows of tubercles, which are completely developed by the fourteenth whorl. Each rib also broadens and loses its definite axial keel.

Discussion. There are few records of the occurrence of this species in Britain. Jukes-Browne (1900 : 50 & 461) listed 5 specimens from the Lower and Upper Gault of Folkestone and Casey (1961 : 601) has recorded it from the Mammilatum Zone. *M. trimonile* is easily distinguished from *M. ornatissimum* (Deshayes) by the presence of three, instead of two tubercular spirals.

After comparison with topotype material Stoliczka (1868 : 199) described this species from the Arrialoor group (Maastrichtian) of Southern India. Although the Indian forms are undoubtedly very similar, Pčhelincev (1953 : 190) considered that they were narrower and showed more strongly differentiated ornament. On these grounds, and because they also occurred at a much higher horizon, he renamed Stoliczka's material as a new species, *M. stoliczkai* Pčhelincev, 1953. Collignon (1949 : 37) indicated this possibility when comparing some very small cerithid specimens from the Albian of Madagascar, with *M. trimonile*.

Pčhelincev, also described another species, *Metacerithium amudasiensis* (1953 : 188, pl. 33, figs 5–12) from the Senonian of Central Asia, that is very similar to *trimonile*. He distinguished this new species by its slightly wider and more rounded sutural area and the fact that the whorl outline is a little more convex. The Upper Cretaceous species, *Metacerithium abictiforme* (Wanner, 1902) described from the Western Desert of Egypt and given a Danian age (Abbass 1963 : 51) is closely related to these species.

Two Albian species from the Perte-du-Rhone also have ornament which resembles that of *M. trimonile*. *Cerithium derignyanum* Pictet & Roux (1849 : 277, pl. 27, fig. 4) has three rows of tubercles with those of the anterior row being the largest, while *Cerithium rhodani* Pictet & Roux (1849 : 279, pl. 27, fig. 6) although having three prominent cords, has tubercles on only two of them.

The considerable variation in the basic ornamental features of the specimens described here as *M. trimonile* is particularly noticeable. Such variation occurs in the relative strength of the tubercular rows; slight positional changes of these rows; alteration in the shape of the tubercules; variation in the strength of the secondary spirals and the collabral threads and in the development of either cancellate ornament, or axial ribs. At present, the extent and significance of these differences is not understood and consequently all such forms are regarded as *M. trimonile*.

Several specimens found in the Gault at Folkestone have features between those of *M. trimonile* and *M. ornatissimum*. BM(NH) G 73793 (pl. 4, figs 1 & 6) is ornamented by two strong tuberculate carinae, with the anterior one being slightly more prominent. The tubercules are somewhat circular on early whorls but become slightly elongate on the body whorl. The concave whorl surface between the carinae is ornamented by opisthocline growth lines that accentuate the tubercules of the anterior row. The lack of a third row of tubercules separates this specimen from typical *trimonile*, while the deep furrow at the suture distinguishes it from *ornatissimum*.

GSM 1698 and SMB 32518 are two examples (pl. 5, figs 4 & 11) that have a closer similarity to *ornatissimum*. Both specimens have a row of tubercles occurring on fairly wide, rounded convex cords close to the adapical and abapical sutures. In the Survey specimen, the tubercles of the posterior row are elongated axially, while those of the anterior row are opisthocline. In SMB 32518, the tubercles are very rounded and strong. Spiral cords cover both whorl surfaces and in GSM 1698 contribute to the cancellate ornament occurring on the narrow interspace between the two primary cords.

GSM 93725 (pl. 5, fig. 6) also has two rows of tubercles (a row situated close to each suture) but in this specimen the tubercles are not prominent and the outline of later whorls is somewhat convex. There is an indication of a third, central, line of tubercles on some of its whorls, which may mean that this specimen is an eroded *M. trimonile*, although apart from the tubercles, the whorl surface appears to be quite smooth.

Metacerithium ornatissimum (Deshayes), 1842

(Pl. 4, figs 5 & 12)

1842 *Cerithium ornatissimum* Deshayes, in Leymerie: 14, pl. 17, fig. 10.
1843 *Cerithium ornatissimum* Deshayes, d'Orbigny: 370, pl. 230, figs 10 & 11.
1852 *Cerithium mosense* Buvignier: 42, pl. 29, figs 10–13.
1862 *Cerithium ornatissimum* Deshayes, Pictet & Campiche: 290, pl. 71, fig. 10.
1862 *Cerithium mosense* Buvignier, Pictet & Campiche: pl. 71, fig. 11.
1864 *Cerithium ornatissimum* var. Seeley: 89.
1900 *Cerithium ornatissimum* Deshayes, Wollemann: 169, pl. 8, fig. 6.
1906 *Metacerithium ornatissimum* (Deshayes) Cossmann: 55, pl. 6, fig. 28.

MATERIAL AND LOCALITY. A number of crushed internal moulds from the Grey Chalk of Dover, Kent, BM(NH) 48152 and G 4315; BM(NH) G 28908, G 74483 from Merstham, Surrey: GG 5601, Varians Zone, Aston Clinton, Bucks.; G 23506, Varians Zone, Chilton, Berks.; 34540 & 8655, Chalk Marl, Hamsey, nr. Lewes, Sussex.

OTHER OCCURRENCES. Kennedy (1969 : 534) records 4 specimens from Band 2 of the Middle Cenomanian, at Bluebell Hill, nr. Burham, Kent. *M. ornatissimum* is described as common in the Gault of France (Departments of the Aube and Meuse); the type coming from Racines, N.W. of Ervy. Wollemann (1900) lists the species from Hildesheim, in N.W. Germany and Pictet (1862) mentions it in the Gault of Switzerland.

DESCRIPTION. Medium-sized, conical shell that it slightly coeloconoid. Its whorl outline is flat to feebly concave and the whorls are three to four times wider than high. The suture is partly obscured by the ornament, but appears to be impressed, or slightly grooved.

The early whorls are not sufficiently well-preserved to determine their ornament. On later whorls a row of tubercles forms an astragal at both the adapical and abapical sutures. Frequently the posterior (adapical) row obscures the other. The tubercles are more prominent, regular and compact on the adapical row and slightly axially extended across the width of the ridge produced. A shallow groove may demarcate the boundary of this adapical row. On the abapical astragal the tubercles are fewer in number and in some specimens, extend adaxially, crossing the interspace between the two tubercular rows and almost reaching the adapical astragal. These rib-like extensions follow the opisthocline growth lines.

The entire whorl surface, including the tuberculate astragals, is ornamented by spiral cords and these vary considerably in thickness and number. These cords together with the opisthocline growth lines produce a cancellate ornament.

On adult specimens the abapical row of tubercles tends to disappear, becoming reduced to a sharp carina that is notched by the numerous oblique growth lines that cross it (see d'Orbigny; Seeley; Wollemann). The flat, slightly convex base below this carina is relatively smooth and only ornamented by the sinuous growth lines. The aperture is not completely preserved, but earlier accounts have described it as angular, or quadrangular, with a straight canal that is curved at its end.

DISCUSSION. All of these British specimens have been found in the Cenomanian, *Schloenbachia varians* Zone of S.E. England. Jukes-Brown (1900 : 192, 203 & 561) has recorded specimens from the *varians* and *subglobosus* Zones of Cambridgeshire, Bedfordshire and Hertfordshire. Only Seeley (1864 : 89) has described this species in Britain and he considered that his examples were a distinct variety.

Wollemann (1900 : 169) concluded that it was impossible to separate *C. ornatissimum* Deshayes from *C. mosense* Buvignier. In this paper, *C. mosense* is regarded as a synonym of *M. ornatissimum*, for the minor differences mentioned by Buvignier (1852) and Pictet & Campiche (1862) are insufficient to exclude *C. mosense* from the range of variation seen within specimens of *M. ornatissimum*. In fact, the two figures shown by Pictet and Campiche are very similar. Their comment on the differing stratigraphical occurrences of the two forms is ill-founded, since only moulds were available from the lower horizon for comparison with *ornatissimum*. However, their dubious observation of 'traces de dents variqueuses' in *ornatissimum* (p. 294) probably convinced them that two species were involved. In shells that are coeloconoid (i.e. the spiral angle changes with growth) it is not possible to distinguish fossil species on slight changes in spiral angle, as Pictet & Campiche attempted.

The growth lines and ornament show that *M. ornatissimum* is comparable to the type species *M. trimonile* and with *M. turriculatum*. It differs from *M. trimonile* in having two rows of tubercles rather than three and in that these rows form strongly rounded astragals. Such a difference is essentially one of ornament style and is best understood from the illustrations (see pls 4 & 5).

Stolizcka (1868 : 200) considered his Cenomanian species, *Cerithium fertile* (pl. 15, figs 11 & 12), from Southern India, as being very close to *M. ornatissimum*. The higher whorls of *C. fertile* enabled him to distinguish the two species while its additional ornament of two rows of smaller tubercles in the centre of the whorl supported this view.

Cerithium sabaudianum Pictet & Roux (1849 : 279, pl. 27, fig. 5) from the Gault of Saxonet, Switzerland, also bears some resemblance to *M. ornatissimum*, in having a tubercular astragal at each suture and would only appear to differ in that the spiral angle is much smaller.

Another closely related species *Cerithium delpeyae* Collignon (1949 : 36, pl. V, fig. 9) from the Albian of Madagascar can be distinguished from *ornatissimum* by the central position of its second abapical row of tubercles.

The two species described by Pčhelincev (1927), *Metacerithium dentatum* (p. 165, pl. 4, fig. 29) and *M. renngarteni* (p. 282, pl. 9, fig. 3) from the Lower Cretaceous of the Crimea and Caucasus are so poorly figured that it is impossible to make any comparison with them. The shape of the latter suggests that the species has been incorrectly identified as *Metacerithium*.

***Metacerithium*? sp. nov.**

(Pl. 4, fig. 9)

MATERIAL. Sedgwick Museum, B 32530 from the Albian, Gault of Folkestone, Kent.

DESCRIPTION. Small, almost smooth, broadly conical shell. The whorl outline is slightly convex with a low anterior carina. Linear, subcarinal and superficial suture. A single poorly-preserved specimen that only shows part of the ornament of its last three or four whorls. There are ten to twelve fine, equal spiral cords separated by interspaces that are equal to the width of the cords. Fine thread-like opisthocline growth lines that have a shallow sinus, cross these cords producing a cancellate ornament. Only the growth threads occur on the convex base. The aperture is not present.

DISCUSSION. This species is provisionally included in the genus *Metacerithium* on the basis of its general shell shape and the similarity of its base and growth lines to other species of this genus. Its distinguishing convex whorl outline might be due to the vagaries of preservation but its lack of strong tuberculate spiral ornament does appear to be a more definite feature. *Metacerithium dentatum* Pčhelincev 1927 (:165) is also said to be smooth, but as previously mentioned, it is so badly figured that further comparison is not possible.

Genus ***CIMOLITHIUM*** Cossmann, 1906

1906 *Cimolithium* Cossmann: 57.
1934 *Cimocerithium* Cossmann, Nagao: 254.

Type species. By original designation (Cossmann, 1906 : 57), *Cerithium belgicum* Münster (1844, pl. 174, fig. 5) from the Tourtia (Cenomanian), at Tournai, Belgium.

Cossmann defined this genus as consisting of moderately large turriculate shells, with flat to concave whorl sides ornamented by a row of tubercles immediately below the suture and having a quadrangular aperture. He was uncertain as to the existence of an anterior canal, but Wenz (1939 : 735) mentioned a weak canal, while Allison (1955 : 419) described a moderately long and straight canal in his species *C. eleanorae.* If the latter is correct, there must be some doubt about its inclusion in the Procerithiidae.

Only the type species *C. belgicum* (Münster), 1844, of those listed by Cossmann (1906 : 58) in his original description of *Cimolithium* can still be included in this genus with certainty. The relationship of the others is doubtful and requires further investigation. *C. inauguratum* Stoliczka (1867 : pl. 15, figs 19, 20) could be a *Campanile*; *C. hispidulum* Stoliczka (1867 : pl. 15, figs 16–18) has some resemblance to the Tertiary genus *Brotia*; and after consulting a figure of the holotype of *C. gallicum* d'Orbigny 1843, in Guéranger (1867, pl. 14, fig. 5) it is doubtful whether that species is a *Cimolithium.*

Occasional examples of this genus occur in widely separated areas, e.g. Western Europe, Japan and U.S.A., during the Aptian and Cenomanian. The specimens described below are the first indication of the occurrence of the genus in Britain.

Cimolithium ascheri (Wollemann) 1908

(Pl. 2, figs 6, 7, 9, 10)

1908 *Cerithium ascheri* Wollemann: 180, pl. 13, figs 8 & 9.

Holotype. Original number 414–415 in the Geologisch-Palaeontologisches Institut der Georg-August Universität, Göttingen; Neocomian, from Bohnenkamp nr. Querum, Sarstedt, North Germany.

Material and horizon. Speeton Clay, Hauterivian-Barremian. BM(NH) G 67942 (no history recorded); GG 20820, Cementstone Group (Barremain), Cayton Bay, Yorks.; GG 20821, C1 or B beds (Hauterivian-Barremian), Black Cliff, Speeton, Yorks; GG 5944 (Hauterivian) C8, Speeton, Yorks; GG 6269 (Valanginian-Berriasian) D1, Speeton, Yorks.; G 55359, (Barremian) B Beds, Speeton, Yorks.

Description. Shell of medium size; initially, spire acutely conical and whorls a little convex, but later whorls progressively increase in diameter producing a rather coeloconoid shell. The whorl has an angular edge at its base. The early whorls are missing on all available British specimens, but the first preserved whorls (presumably the 4th and 5th after the protoconch) are very slightly convex and bear rounded axial ribs. These ribs are opisthocline, are separated by constricted interspaces and follow the growth lines. On the next visible whorl (in GG 20820) the ribs are lost and only the growth lines and two tuberculate astragals occur, the larger one at the adapical suture and the smaller one abapically. The astragals are formed by a linked series of rounded tubercules.

The whorl outline between the astragals gradually becomes more concave. Faint spiral threads occur on each whorl. Initially, the growth lines are opisthocyrt, but become opisthocline and on the slightly rounded base of the last whorl they can be seen to arch forward. Little of the aperture is preserved in these specimens, but it is thought to have a broad sinus and to be rather quadrangular. It also appears to have a calloused parietal lip and a suggestion of a posterior channel. The extent of the anterior canal is not known.

Most of the specimens from the Speeton Clay have lost their ornament and have flat to slightly convex whorl outlines. In GG 20820, the ornament has been preserved, and this shows a grooved linear suture between the noded abapical and adapical astragals of adjacent whorls.

Discussion. Wollemann commented that the ornament of his new species was similar to that of *Cerithium sanctaecrucis* Pictet & Campiche, (1864 : 283, pl. 70, fig. 14). Ascher (1906 : 148) mentioned the confusion that has arisen in distinguishing that species and both *C. terebroides* d'Orbigny (1842 : 352) and *C. ricordeanum* Cotteau, (1854 : 43). Cossmann (1906 : 48) included them all in his genus *Terebrella*, which he placed in the sub-family Paracerithinae. This may have been the reason that caused both Allison (1955 : 419; *C. eleanorae*) and Nagao (1934 : 254, *C. miyakoense*) to overlook the similarity of their species to *Cerithium ascheri*. In fact, it is this resemblance of ornament together with its general shell shape, which suggests that *Cerithium ascheri* belongs to the genus *Cimolithium*.

This early species of *Cimolithium* with a carina at the edge of the base, differs from *Gymnocerithium* which possesses a more rounded base and in this respect resembles *Metacerithium*. However, both the BM(NH) material and Wollemann's holotype (kindly sent on loan for comparison by Dr S. Ritskowski, of Göttingen) show a thickened inner lip, as occurs in *Gymnocerithium*. The quadrangular aperture of *C. ascheri* readily distinguishes it from that genus, while its ornament of noded astragals and the less pronounced anterior canal (in contrast to a curved beak-like shape) serve to separate it from *Metacerithium*. Yet, other features, such as the numerous narrow whorls, the general coeloconoid shape and the small apertural posterior neck, are similar to those found in *Metacerithium*.

The comparable shell shape and ornament of the Aptian *Cerithium sanctaecrucis* Pictet & Campiche (1864 : 283, pl. 70, fig. 14) indicates that this species is another early *Cimolithium*. The relationship and distinctions between it and both *C. terebroides* d'Orbigny and *C. ricordeanum* still need to be verified by examining type material, but they can all be distinguished from *C. ascheri* in that they only have one noded astragal.

Another slender, turriculate species, *Cimolithium elaneorae* Allison (1955 : 419) from the Middle Albian of Mexico, has two noded astragals but can be recognized by its additional ornament of strong axial ribs. The early whorls of the Japanese Aptian species *Cimolithium miyakoense* Nagao, (1934 : 254), have prominent axial ribs, but later, these are reduced to a series of adapical and abapical nodes. However, in *C. miyakoense* var. *tomasensis* Allison, 1955, the axial ribs are persistent, while the whorl diameter progressively increases to give a somewhat coeloconoid shape as occurs in *C. ascheri*.

The Cenomanian *C. belgicum* from Tournai, differs from *C. ascheri* in that it is essentially much larger, being at least twice the size of the latter; has only one visible row of nodes, of which there are fewer per row than in *ascheri*; its fine spiral threads are wider apart while the growth lines are finer and more opisthocyrt than those in *C. ascheri*.

Cimolithium komarense Pčhelincev, 1927 (pl. 4, fig. 32) from the Lower Albian of the Crimea, is based on a fragment of two whorls, which show an angular basal edge and a row of small subsutural tubercles. It is therefore impossible to make any useful comparison with this almost indeterminate specimen.

***Cimolithium* aff. *eleanorae* Allison, 1955**

(Pl. 2, fig. 5)

MATERIAL. BM(NH) G 74550. Cenomanian, between Charlton Bay and Culverhole Point, E. Devon.

DESCRIPTION. Medium-sized shell; high-spired, slender and turriculate, linear adpressed suture, which, appears to undulate as it abuts against axial ribs of the previous whorl. Whorl outline flat. The early whorls are not preserved. On later whorls, a series of about twenty elongated tubercles occurs just below the adapical suture and these have interspaces greater than their width. The tubercles form a slight astragal, which is approximately a quarter of the whorl height. The remainder of the whorl is ornamented by a smaller number of axial ribs and numerous very fine spiral threads that are at least twice the width of the interspaces between them. The axial ribs increase in number on successive whorls, some coincide and join with the adapical tubercles but the majority alternate with them, taper posteriorly and stop short. These ribs are slightly opisthocline, with the odd one markedly so. They are irregularly spaced and occasionally two occur very close together, only separated by a growth line. The growth lines are opisthocyrt. The base of the whorl is convex, but its ornament is not preserved, although the growth lines can be seen to curve narrowly forward and down on to the short anterior canal. The aperture appears to be ovate. Measurement of this partly worn and incomplete specimen has not been considered worthwhile.

DISCUSSION. There is a distinct resemblance between this specimen and *Cimolithium eleanorae* Allison, from Mexico. However, the British Cenomanian fossil has a more acute spire than the Mexican specimen and also lacks its abapical angular whorl edge. In addition, its whorl sides are undoubtedly flat and axial ribs appear to be present on all whorls. Unfortunately, incomplete preservation prevents any exact comparison of the number of tubercles, ribs and spiral threads, or the extent of the anterior canal, although the aperture is ostensibly similar. *Cimolithium miyakoense* Nagao (1934) would seem to be rather broader than *C. aff. eleanorae* and its axial ribs are lost on later whorls, while it also possesses a series of tubercles abapically on the body whorl. The variety *C. miyakoense tomasensis* Allison (1955) lacks the adapical row of nodes and is also broader.

Cimolithium belgicum (Münster) 1844, (fig'd. Cossmann 1906 : pl. 14, figs 2–3 bis) can be distinguished from *C. eleanorae* by a lack of axial ribbing on the later whorls and also by being somewhat broader.

?Genus ***RHABDOCOLPUS*** Cossmann, 1906

TYPE SPECIES. By original designation, *Melania scalariformis* Deshayes, (1830 : 427); figured by Eudes-Deslongchamps, (1842; pl. 11, fig. 63).

DISCUSSION. As yet, it has not been possible to assign the species of Procerithiidae described below to any recognized genera with any certainty.

In some respects their ornament is similar to that of the Bajocian species *Cerithium millepunctatum* Deslongchamps, 1842 from Bayeux, included in *Procerithium* by Cossmann (1906 : 25), but apart from this general resemblance, the rounded aperture and the stratigraphical occurrence of this latter genus, ends any further comparison.

Cossmann (1906 : 57) included one of these species, *Cerithium forbesianum* d'Orbigny, in his original description of the genus *Uchauxia*. Yet, accepting that *Uchauxia* has a rounded aperture and a short anterior canal, the aperture present in *forbesianum*, although rounded, shows no indication of a canal, nor of the irregular varices which also characterize that genus.

Ornamental similarity, again invites comparison with the Cenomanian genus *Voysa*, described by Stephenson (1952 : 169, pl. 39), which he referred to the family Cerithiopsidae. The concave trend of the growth lines on the upper part of the whorl is analagous to that present in the species mentioned here, but although there is a considerable variation in both ornament and form of the species ascribed to *Voysa* not one possesses a whorl outline or a grooved suture that is exactly comparable to those of either *Cerithium clementinum* or *C. forbesianum*.

Among genera included in the Procerithiidae, the various features shown by members of the genus *Rhadbocolpus* Cossmann, 1906, bear the greatest likeness to this Cretaceous material. [*Rhabdocolpus* is considered a separate genus following Haas (1953 : 233), rather than a subgenus of *Procerithium* as originally proposed by Cossmann (1907 : 27)]. However, the distinctive ornament of *Rhabdocolpus* described by Haas, consisting of dominant axial ribs and an adapical 'coronet' formed by the tubercles on the adapical ends of the ribs, would appear to deter any further comparison. In his investigations of Peruvian Triassic material, Haas distinguished two groups within members of *Rhabdocolpus* and it is possible to make a similar distinction between later Mesozoic representatives. One group consists of slender shells typified by the Kimmeridgian *R. quehenensis* (de Loriol) and another is comprised of those forms with more rounded whorls and opisthocline axial ribs that are comparable to the Bajocian *R. undulatus* (Eudes-Deslongchamps).

Such morphological diversity occurs in later forms and contributes to the difficulties experienced in classifying them, e.g. Cossmann (1906) was not satisfied with his own assignation of several species to the genera he recognized in the Procerithiidae. Similarly, the controversy over the recognition of some Upper Jurassic and Lower Cretaceous marine and brackish water forms as Melaniidae, or Procerithiidae (see Arkell, 1941 : 95–100 and Huckriede, 1967 : 188–189) provides further evidence of this difficulty in their determination. It would seem that a greater variety than hitherto suspected, occurs within the forms referred to as *Rhabdocolpus* and that the existence of these groups awaits determination. Further investigation will probably lead to these sub-groups being accepted as sub-genera.

The ornament of *C. clementinum* d'Orbigny, Forbes could be derived from that of the Bajocian *P.* (*R.*) *granulatocostatum* (Münster), figured in Cossmann, (1913 : pl. 4, figs 11–12). The predominance of spiral over axial ornament seen in ?*R. forbesianum*, first occurs to a lesser extent in *R. manselli* (de Loriol), which suggests that this species may be an ancestor of *forbesianum*. This dominance of spiral ornament caused Haas to doubt whether *R. manselli* belonged to *Rhabdocolpus*.

Finally, the occurrence of at least two and possibly three species, of ?*Rhabdocolpus* at one horizon in the Lower Greensand [Crackers], requires further consideration and palaeoecological interpretation.

Haas, after investigating South American Triassic material, concluded that the relationship of the genera *Protofusus*, *Paracerithium* and *Rhabdocolpus* is much closer than that implied by Cossmann's classification, although as he pointed out (pp. 212 & 293), their exact position can only be discovered from a thorough investigation of all Triassic Procerithiidae. He showed that the morphological changes occurring in these genera, particularly in their ornament, could be interpreted as a series, with *Rhabdocolpus* the most highly specialized of the three. However, the evidence and determination of the earliest representatives of these genera is confusing and such a lineage remains doubtful. A further complication is the close resemblance, especially of ornament, of *Rhabdocolpus* to the Triassic genus *Andagularia* Haas, which is considered to belong to the Purpurinidae.

?***Rhabdocolpus*** ?***clementinum*** (d'Orbigny)

(Pl. 5, figs 6, 12 & 13)

?1843 *Cerithium clementinum* d'Orbigny: 357, pl. 228, figs 1–3.
1845 *Cerithium clementinum* d'Orbigny; Forbes: 352, pl. 4, fig. 9.

MATERIAL, LOCALITY AND HORIZON. BM(NH) GG 5692–5694, GG 20841–20843, GG 20844 (5), Crackers, Lower Greensand; GG 5708 (5 specimens), Lower Lobster Bed, Lower Greensand; Atherfield, Isle of Wight.

DESCRIPTION. A very small, turriculate shell with a narrow spire, flat-sided whorls and a grooved linear suture. The whorls are ornamented by 16–20 axial ribs, that are orthocline on the early whorls but soon become strongly opisthocline. Generally, five primary spiral cords are visible on the whorl side, with occasionally a secondary cord between the second and third. Small rounded tubercules occur at the intersections of the axial ribs towards the base of the whorl; these tubercules become somewhat rectangular on the abapical cords.

The base is convex and has a varying number of spiral cords ornamenting its surface, although there are always a pair of primary cords forming small carinae some distance from the periphery and another pair of strong cords close to the columella. The entire semi-rounded aperture is flat at its base and has a straight inner lip.

In complete specimens, the growth lines are visible on the body whorl and these are initially strongly prosocline, but at the second spiral cord swing back to become strongly opisthocline, producing a rather asymmetric opisthocyrt shape.

Discussion. Unfortunately, it has not been possible to discover Forbes' original specimen in the Geological Survey Collection. The various specimens from the same locality listed above, bear a strong resemblance to his figure of a turriculate, gastropod with cancellate ornament. Judging from the specimens in the British Museum (Natural History) collection, it would appear that in his figure, the ribs are too numerous, and that the dimensions of the whorls are incorrectly drawn.

The only other figures of *C. clementinum* are those given by d'Orbigny (1843 : 357, pl. 228, figs 1–3) and these do not show the typically cancellate and tuberculate ornament of the British specimens. D'Orbigny's figures show smooth cords and ribs that are orthocline, or only opisthocyrt rather than the strongly opisthocline ribs of the British Aptian fossils. In fact, d'Orbigny's figure could equally as well be interpreted as an attempt to represent the ornament of *C. forbesianum* d'Orbigny [= *C. phillipsi* Leymerie of Forbes].

Wollemann (1900 : 169) suspected that Forbes' Aptian fossil was not identical to those described by d'Orbigny from the Neocomian of Marolles (Dept. d'Aube), although he did not explain his doubts. In his description of *C. clementinum*, he mentioned that the axial ribs of subsequent whorls are irregularly alternate and that the whorls are convex, while he described the aperture as being quadrangular and depressed. Such a description could not be applied to the specimens referred here to Forbes' 1845 figure.

It is not advisable to introduce a new specific name for the British material, until d'Orbigny's material has been re-examined and his types recognized. Peron (1900 : 192) commented that the ornament of *C. clementinum* is extremely variable and that the specimen figured in the '*Paléontologie française*' is a very rare form.

? ***Rhabdocolpus forbesianum*** d'Orbigny, 1850

(Pl. 5, figs 1–5)

1845 *Cerithium phillipsi* Leymerie; Forbes: 352, pl. 4, fig. 12.
1850 *Cerithium forbesianum* d'Orbigny: 116
1854 *Cerithium forbesanum* d'Orbigny; Pictet & Renevier: 52, pl. 5, fig. 6.
1864 *Cerithium forbesianum* d'Orb.; Pictet and & Campiche; 286.

1868 *Cerithium forbesianum* d'Orb.; Verneuil & Lorière: 15, pl. 2, figs 7a–e.
1906 *Uchauxia forbesiana* (d'Orb.); Cossmann: 57 & 252.
1961 *Uchauxia forbesiana* (d'Orb.); Casey: 607.

MATERIAL AND OCCURRENCE. Four specimens in the collections of the Geological Survey Museum have been accepted as the original material in the Geological Society Collection that was described by Forbes (1845) as *C. phillipsi*. Two of the specimens bear the Geological Society number 2267 and the other two are associated with a label numbered 2275 and all are from the Lower Greensand of Atherfield, Isle of Wight. Blake (1902) lists R 2267 in his catalogue of type material at the Geological Society and, it is true, that a specimen with this number in a small rock fragment, bears ornament similar to that shown in the original figure on Forbes' plate 4. However, not one of these specimens is exactly like the figure, which is probably a composite representation of the features shown by these incomplete and poorly preserved specimens. This material must, therefore, be accepted as a type series and one of them, GSM Geol. Soc. 2275 (a)—an incomplete specimen but clearly showing the ornament of later whorls,—is selected here as a lectotype.

I have used better preserved, topotype material from the Crackers, Lower Greensand, in the British Museum (Natural History) collections to describe this species; GG 20845–20849, GG 20850 (6), GG 5609, GG 5695–5697, G 20898 and G 20908. Another specimen G 20983 comes from East Shalford in Surrey, an Atherfield Clay locality mentioned by Casey (1960 : 547).

DESCRIPTION. A very small shell (on average 2–4 mm in height), composed of convex whorls that are separated by a grooved linear suture; in the early whorls the suture may appear to undulate owing to the effect of the axial ribs. The ornament of the early whorls is quite different from that of the later whorls. Initially, ornament consists of several spiral cords and 10–14 opisthocline axial ribs, with slight tubercules occurring where the cords cross the ribs. After 3 or 4 whorls the axial ribs disappear but continue to influence the cords, first as the tubercules briefly persist and then by producing slight crenulations and, or, thickenings in the smooth ribbon-like spiral cords. On later whorls, six raised-primary cords are generally visible but some variation in this number occurs. Frequently, the third and fourth cords from the adapical suture are the strongest and these occur at the centre of the whorl. In other examples, the strongest cords occur towards the abapical suture with the weakest on the adapical shelf. The interspaces between the spirals are considerably wider than the width of the cords. Secondary cords develop in these interspaces, but not according to any definite pattern.

The rounded base is ornamented by a varying number of spiral cords with a primary cord close to the periphery and two other primary cords close to the columella. Growth lines are only visible on the whorl sides as striae between the cords, but they are easily seen on the base and swing back towards the columella.

The semi-rounded aperture is entire, has a flat basal lip, a thin outer lip, straight inner lip and a smooth columella.

DISCUSSION. Several authors have followed d'Orbigny and used the name *forbesianum* to describe this British Aptian fossil, but few have endeavoured to distinguish it from *Cerithium phillipsi* Leymerie 1842. D'Orbigny first used the name *forbesianum* in his Prodrome (1850 : 116) when recording the British material, which he considered Forbes had misidentified, but did not provide any detailed explanation. Pictet and Campiche (1864 : 287) suggested that the slender elongate form of both species may have led to the confusion, but commented that the rare varices that occurred in *C. phillipsi* provided an easy method of distinguishing the two species. These varices are easily seen in d'Orbigny's figure of the French species (1843 : pl. 227, fig. 10) but are not shown in Leymerie's own figure (1842 : pl. 17, figs 11a & b) of this more elongate shell. Verneuil and Lorière (1868 : 15) recognized that *C. forbesianum* was quite different from *C. phillipsi* and provided the only adequate figure (pl. 2, figs 7a–e) of the species to show its variable ornament, when describing its occurrence at several localities in the Aptian of the Spanish province of Teruel.

Çossmann (1906 : 57) obviously accepted, or also observed, the varices in *C. phillipsi* Leymerie, for he included the species in his new genus *Uchauxia* in which the possession of varices is a diagnostic feature. Yet, this evidence still needs to be verified by examining type material, and, in order to ensure that *phillipsi* does belong to *Uchauxia*, it is also necessary to ascertain that an anterior canal is present for one has not been figured. At the same time, Cossmann (1906) referred *C. forbesianum* to *Uchauxia* commenting that it was close to *phillipsi* and quoted Pictet as his source. The only figure produced by Pictet is that in Pictet and Renevier (1854 : pl. 5, fig. 6) which depicts a shell with ornament between that of *forbesianum* and *phillipsi* [as understood from the figures quoted above]. However, the presence of an entire aperture in several of the British specimens of *forbesianum* listed above, shows that this species cannot belong to *Uchauxia* (as interpreted by Cossmann, 1906).

The turreted and flat-sided whorls of *C. clementinum* d'Orbigny; Forbes, together with their persistent cancellate ornament, easily distinguish this species from the differently ornamented *forbesianum* with its strong spiral cords and convex whorls. Yet both have several features in common, such as a grooved linear suture, and a semi-rounded entire aperture, while their early whorls can be confused if the ornament is not adequately preserved.

The greater convexity of the whorls and their persistent orthocline axial ribs distinguish *C. dupinianum* d'Orbigny (1843 : 357, pl. 227, figs 4 & 5) a similar species to *forbesianum*, described from the Neocomian of Marolles (Dept. d'Aube).

? ***Rhabdocolpus melvillei*** sp. nov.

(Pl. 5, fig. 7)

DIAGNOSIS. A small procerithiid with reticulate ornament on its early whorls but which loses axial ornament on later whorls, and has a wider spiral angle than usual in the genus.

HOLOTYPE. In the Sedgwick Museum, B. 27340.

OTHER MATERIAL. Four paratypes in the Sedgwick Museum, Cambridge, B. 27341–27344, all belonging to the Wiltshire Collection.

Locality and horizon. Crackers, Atherfield Clay Series, Lower Aptian, Forbesi Zone, near Atherfield Point, Isle of Wight.

Description. The shell is very small and has a wide spiral angle. The whorl outline is strongly convex and the suture impressed. The earlier whorls show about twelve opisthocyrt axial ribs. On later whorls, three spirals appear and small rounded tubercles are developed where these intersect the axials. Later, a gap develops between the first and second spiral cords and two further cords are produced on either side of the first. The new spirals eventually become as strong as the earlier formed ones. On the body whorl, the spirals are separated by interspaces greater than their width and the axials are separated by interspaces greater than those between the spirals. The rounded base is ornamented by several less-tuberculated spiral cords.

Discussion. This species can be distinguished from ? *R. forbesianum* by its more strongly-rounded whorl outline, by its greater number of axial ribs, slightly stronger development of tubercles and wider spiral angle. The few specimens of ? *R. melvillei* that are available do not show any indication of secondary spirals between the primaries, nor the marked differentiation in ornament that occurs in *forbesianum*. However, the full range of variation within *forbesianum* is not known and it could be possible that ? *R. melvillei* is, merely, a variety of that species.

Family ? **PROCERITHIIDAE**

Genus ? ***UCHAUXIA*** Cossmann, 1906

Type species. By original designation Cossmann (1906 : 56), *Cerithium peregrinorsum* d'Orbigny 1843, from the Turonian of Uchaux, Vaucluse, France.

Discussion. The material described below, undoubtedly belongs to a common genus and because of considerable similarity in form and ornament to species of *Uchauxia*, they are regarded as belonging to that genus. However, owing to their incomplete preservation this determination must remain provisional.

The genus *Uchauxia* is also subject to uncertainty, for a crucial factor in its recognition is the apertural shape of its type species, *U. peregrinorsa*. The various figures of that species provided by d'Orbigny (1843 : pl. 231, fig. 3), Cossmann (1906 : pl. 6, figs 37–40) and Roman and Mazeran (1920 : pl. 5, figs 42–44) do not provide sufficient reliable evidence of this feature, although each author mentions a rounded aperture with a short anterior canal in his description. In order to verify these features it is necessary to refer to the type material. Unfortunately, this has not been possible during this investigation, nor have other specimens of the species been available for comparison.

For the moment, following Cossmann (1906 : 57), it is assumed that these small Cretaceous shells are fully grown and that they resemble *Procerithium* and *Rhabdocolpus*, but have a distinct, short anterior canal.

Uchauxia, as here understood, is generally larger than *Cerithiopsis* Forbes & Hanley but does have a similar whorl shape and tends to have the same range of ornament. *Cerithiopsis*, however, usually has a more advanced type of siphonal canal, which does not project above the basal plane and resembles a keyhole in basal view. Cossmann (1906 : 57) pointed out that *Uchauxia* only occurs in strata that are believed to be entirely marine and for this reason, differs from both *Potamides* Brongniart 1810 and *Pirinella* Gray, 1847.

Uchauxia wisei sp. nov.

(Pl. 6, figs 5 & 6)

DIAGNOSIS. *Uchauxia* with four prominently beaded spirals, the abapical penultimate spiral being weaker than the others, and weakly developed axial ornament.

HOLOTYPE. BM(NH) GG 6161, C. W. Wright collection.

OTHER MATERIAL. Eight Paratypes BM(NH) GG 5611, GG 6158–6160 & GG 6162–6165. C. W. Wright collection. All incompletely preserved.

LOCALITY AND HORIZON. Claxby Ironstone, Valanginian-Hauterivian, Nettleton, Lincs.

DESCRIPTION. The shell is small, narrow and turriculate, slightly cyrtoconoid, with a flat-sided whorl outline and linear suture. On the earlier whorls, three primary spiral cords are developed with interspaces of equal width. The anterior and posterior spirals become more prominent on later whorls, with the central spiral moving posteriorly as a secondary spiral cord makes its appearance abapically to it. A secondary spiral is also developed behind the posterior primary spiral. On still later whorls, a secondary spiral cord may appear between the two posterior primary spirals. The spirals cross 20 to 24 axial ribs, producing rounded tubercles at each intersection. The axials are separated by interspaces almost equal to their own width and are orthocline on the early whorls but become opisthocyrt.

The base is convex and bordered by two spiral cords; the axials do not extend on to it and the surface is almost smooth. The small, oval aperture has a curved anterior canal. The growth lines follow the axial ridges.

DIMENSIONS. Holotype BM(NH) GG 6161.

Height (approx. 5 whorls)	10·0 mm
Spiral angle	12°
Penultimate whorl height	1·8 mm
Penultimate whorl diameter	3·8 mm

DISCUSSION. The most characteristic feature of this species, when compared with other species of *Uchauxia* that have four spiral cords, is the weak influence of any axial component. In the Turonian type species, *U. peregrinorsa*, the axials are quite strong, and similarly, in the Gosau species *U. solida* (Zekeli, 1852 : pl. 20, fig. 3) and *U. distinctum* (Zekeli, 1852 : pl. 19, fig. 6), the exact age of which needs to be investigated (see Kuhn, 1947 : 188).

U. wisei is distinguished from the two species described below, in that *Uchauxia* sp. nov. has only three spiral cords of tubercles ornamenting the whorl and that its tubercules have some axial alignment; while the prosocline axial ornament of *U. badri* is quite diagnostic.

The specimen described by Roman & Mazeran (1920: pl. 5, fig. 45) as *Uchauxia richei*, although having predominantly spiral ornament, has many more cords, which have a lower degree of tuberculation, than *U. wisei*. Originally, their specimen was figured by Cossmann in his examples of *U. peregrinorsa* and it may still be found to come within the range of variation of that species, when this aspect is fully investigated.

Although the figures of the type species in both Cossmann (1906) and Roman & Mazeran (1920) are inadequate for exact comparison, it is possible to decide that *peregrinorsa* (d'Orb). has several more tuberculate spirals than this specimen of *U. wisei*. The Turonian species described by Roman & Mazeran, *U. richei*, has three granular cords but possesses many more primary cords and has a slightly different whorl outline.

The British Museum (Natural History) collection included a number of *Ageria gaultina* sp. nov. from the Gault of Folkestone, which at first sight, have some resemblance to this fossil but the existence of a greater number of axial ribs and a differing growth line pattern provide adequate distinguishing characters.

Uchauxia badri sp. nov.

(Pl. 6, figs 3 & 4)

DIAGNOSIS. A small, slender, cyrtoconoid, turriculate shell that is ornamented by four tuberculate spiral cords, the tubercules of which are aligned along prosocline axial ribs, giving a distinctive twisted appearance to the shell.

HOLOTYPE. Sedgwick Museum, Cambridge, B 44632.

HORIZON AND LOCALITY. Upper Greensand, Albian, Blackdown, Devon.

DESCRIPTION. A small cyrtoconoid shell with a slender turriculate spire. The whorl outline is slightly convex and the shell has a grooved linear suture. The ornament of the earlier whorls is dominated by strong axial ribs which cross three unequally-spaced spiral cords. On subsequent whorls, the number of cords increases to four and eventually five, producing rounded tubercles at their intersections with the axial ribs. The ribs consequently become less dominant and contribute to the cancellate effect of the ornament. The interspaces between the spiral cords are then equal and also equal to the width of the cords but considerably narrower than the spaces between the axial ribs. The prosocline axial ribs are partly offset in relation to one another on subsequent whorls and this gives a twisted look to the shell. On later whorls, these ribs become reduced in strength, although this may, in part, be due to wear and poor preservation. On the penultimate and body whorl, it is also possible to see the fifth spiral cord, which occurs close to the abapical suture. The axial ribs influence this, but although they may cross it, they then weaken towards the suture.

The convex base is covered by faint collabral threads and ornamented by five spiral cords, two of which produce small carinae. The small rounded aperture has a partly twisted anterior canal.

Dimensions. Holotype, Sedgwick Museum, B 44632.

Height	10·6 mm
Mean spiral angle	20°
Height of last whorl	3·0 mm
Maximum diameter	2·9 mm

Discussion. The distinctive prosocline axial ribs, that give the ornament of this species a slightly twisted look, have been mentioned in the discussion of the preceding species. It is this feature that immediately distinguishes *U. badri* from the type species *U. peregrinorsa* despite the figures of the latter being unsuitable for any further detailed comparison. However, it is also possible to observe that the axial ribs of *peregrinorsa* are opisthocyrt and that its spiral cords are much thinner (i.e. weaker) than those of *badri*.

One of the Lower Cretaceous species, *forbesianum* (d'Orbigny), that Cossmann included in this genus, is now thought to belong to *Rhabdocolpus* Cossmann, 1906. There is still some confusion concerning the characters of *U. phillipsi* (Leymerie) and as suggested elsewhere in this paper, type material needs to be re-examined in order to verify the validity of Cossmann's determination. The ornament shown in the few figures of this slender species is quite different from *U. badri*, but Leymerie's figure (1842, pl. 17, figs 11a & b) although not showing varices, does show orthocline axial ribbing.

Cerithium kaunhoweni Cossmann (1902 : 61), from the Maastrichtian of Maastricht, differs in that, although having cancellate ornament, this is much finer and composed of at least 6 untuberculated spiral cords and numerous opisthocyrt axial threads, while the shell also has a definite anterior canal. *Cerithium distinctum* Zekeli (1852: pl. 19, fig. 6) from Gosau, although having four predominate tuberculate cords between the sutures, also has a thin cord in the centre of each interspace and has strongly orthocline axial ribs.

Uchauxia sp. nov.

(Pl. 6, fig. 7)

Material and locality. BM(NH) G 73788 J. S. Gardner Collection, Gault, Folkestone, Kent.

Description. Unfortunately, this unique specimen is rather crushed and measurements are not reliable, but it has been possible to discover details of the ornament by developing out its reverse side. This gastropod can be described as a small, more or less subulate, slender shell with convex whorls. Its moderately deep, linear suture lies at the bottom of a concave furrow formed by adjacent whorls. The initial whorls show bicarinate ornament, but a third spiral cord soon appears just behind the posterior of the two initial cords, and others develop later. These spiral cords are separated by wider interspaces and each interspace is occupied by at least one almost smooth spiral thread. The primary cords are tuberculate and the rounded tubercles are separated by intertubercular spaces that are nearly equal to their width. Usually these are of the same number and strength on each cord, but sometimes those on the posterior cord are slightly weaker. On the early whorls, the axial ridges are as dominant as the spiral cords, yet, later, with the increase in size of the whorl they appear to become slightly disrupted and if there is any connection at all, only a thin curved ridge joins the tubercules. These ridges tend to follow the opisthocyrt growth lines. Towards the base the whorl flattens repeatedly; first to a serrated cord making a slight carina and then again to another smooth cord. Only the former is visible on previous whorls and would appear to mark the periphery of the whorl. Traces of a short columella and an aperture with a short, shallow anterior canal are present.

DISCUSSION. Cerithiaceans with this general form are common amongst both European and American gastropods and include many marine and non-marine species. However, the Cretaceous age of the specimen and its occurrence in an undoubtedly marine deposit, prompt its inclusion in the genus *Uchauxia*.

The ornament of the specimen serves to distinguish it from both *U. wisei* and *U. badri*. It differs from *wisei* in the number of spiral cords and their interspace width, while the possession of fewer tubercles on each cord and the stronger axial ridges emphasize the differences between the two species. The more reticulate pattern produced by cords, tubercles and ribs, assists in separating it from *badri*, although it is the markedly prosocline ribs of the latter which separate the two species and which give *U. badri* a slightly twisted look.

Family **CERITHIIDAE** Fleming, 1828

REMARKS. Cossmann (1906) discussed the relationship of the Procerithiidae and the Cerithiidae (p. 20–21) and the derivation and evolution (p. 60–61) of the very prolific Cerithiidae in detail. He concluded that the anterior canal was the most important diagnostic character in separating the two families, even though the form of the canal was extremely variable within the Cerithiidae and that the demarcation between the subcanaliculate beak of the Metacerithiinae and the truncated canal of the Potamidiinae would appear to be very slight but quite distinct. In his view, the two families can easily be separated by the character of the canal, for even in the most truncated cerithiid the anterior canal always forms a slight ridge or projection beyond the surface of the base, while conversely, the beak of the Procerithiidae never protrudes below the base of the shell. In the Cerithiidae the canal is also generally twisted.

Although Cossmann was satisfied that the Cerithiidae were derived directly from the Procerithiidae, it is possible that they may have arisen from the Jurassic family Eustomidae (see Cossmann, 1906 & 1913). Members of this family, consisting of the two genera *Diatinostoma* and *Ditretus*, possess a well-marked, but straight, cerithiid-like canal and generally occur in the coral-rudist assemblage at horizons from the Bathonian to the Turonian, (see Cossmann 1906 : 12–14). If this alternative should prove to be correct, the relationship of the Cerithiidae with holostomatous forms might be further apart than Cossmann suspected. On the other hand, the apparent relationship may be explained by homeomorphy.

It is particularly noticeable that from Upper Cretaceous to Recent times, the members of the Cerithiidae have frequently been associated with corals. In the

Cretaceous, the richly coralline areas occurred further to the South and consequently, the British record of the Cerithiidae at this time is very sparse. The available evidence, which undoubtedly suggests that the Cretaceous was a period of experimentation within the family, represents differing degrees of specialisation of the entrance to the mantle cavity and of the anterior siphon. It is interesting to note that typical holostomatous procerithiid forms also occurred at these times but only persisted until the end of the Cretaceous.

Sub-family ? **CAMPANILINAE** Wenz, 1940

Genus ? ***CAMPANILE*** Bayle (in Fischer), 1884

? ***Campanile cenomanica*** sp. nov.

(Pl. 6, figs 1 & 2)

Diagnosis. High, conical shell with whorls ornamented throughout by an adapical carina and three prominent spiral cords; the twisted columella lacks any folds.

Material and occurrence. BM(NH) GG 18686; its history not certain, for although the original label states 'Chalk Marl, Craie Chloritique, Dorset' and gives the registered number 73597, the information in the register given with that number could not appertain to this particular specimen. Its preservation does suggest that it may come from the Cenomanian of Dorset, yet efforts to find similar material both in collections and in the field have not been successful.

Description. Unique turreted, conical, slender shell of medium size that is not completely preserved. Flat whorls, having straight whorl outline with a slight adapical shoulder. Adpressed linear suture. Whorl ornament characterized by a high adapical astragal with a rounded edge and bearing beads that are separated by intervals equal to their own width. Three prominent spiral cords are equally distributed below this and in each interspace there is a faint spiral thread. The central cord is somewhat weaker. Beaded ornament gradually develops on the astragal and on the cords. A fourth, but smooth spiral cord can be seen at the basal edge of the penultimate whorl. This cord marks the limit of the shallow convex base, ornamented by numerous equally spaced spiral cords.

The spiral ornament is crossed by frequent opisthocyrt growth lines, which straighten a little towards the abapical suture, but after crossing on to the base, curve forward and then finally swing back towards the columella. At intervals corresponding to the occurrence of the beaded tubercles, and following the growth lines, there is a slight alteration in the growth direction of the shell.

The poorly preserved aperture is not large in proportion to the remainder of the whorl, as in some species of *Campanile*. It shows a slightly twisted columella with a distinct anterior canal and has a callused parietal lip. There are indications of a small posterior 'gutter' or neck, and the form of the outer lip cannot be interpreted with any certainty.

Discussion. The apertural features shown by this specimen, undoubtedly, indicate a strong affinity with the Cerithiidae. Its ornament and general shell morphology are comparable to those of the genus *Campanile*. However, the apparent atypical growth lines, the shorter anterior canal and lack of columella folds could be interpreted as an indication that it would be better placed in the Cerithiinae. Yet, on referring to the literature, one recognizes that the features generally accepted as those of *Campanile*, because of its Eocene type species *C. giganteum* (Lamarck) 1804, are only one end of the range occurring within that genus. In fact, another Eocene species *C. cornucopiae* (J. Sow.) 1818, is basically very similar to the British Cretaceous specimen, having a sub-rhomboidal aperture, a small twisted anterior canal below a callused parietal lip, initially a flat whorl outline, a linear suture and the same slight straightening of the opisthocyrt growth lines. The presence of two columellar folds is the only difference between the two species.

Two Maastrichtian species from Iran described by H. Douville (1904 : 312, pl. 43), *C. morgani* and *C. breve* show the rather simpler ornament of *C. cenomanica*. Another Maastrichtian species *C. carezi* Vidal, (1917; 7, pl. 3, fig. 6) from Sensui, Spain, has the typical coronet ornament of later species of *Campanile*. All of these, however, possess the distinctive columellar folds of the genus.

Whether the British fossil is a juvenile, the early whorls of an incomplete specimen, or an early form of the genus *Campanile*, remains to be discovered. It certainly does not show the characteristic two fold ornament that develops in Tertiary species of the genus. More material is also necessary before one can attempt to investigate its relationships with other Cretaceous species, or to make any conclusions as to its possible position in the evolution of the campanilids. Cossmann recognized that the genus first appeared towards the end of the Cretaceous, but *C. cenomanica*, if correctly identified, would probably place their origin farther back than he suspected.

Genus ***EXECHOCIRSUS*** Cossmann, 1906

Type species. By original designation, Cossmann (1906 : 121), *Cerithium cingillatum* Zekeli, 1852 (pl. 18, fig. 6), from the Upper Cretaceous of Austria.

Description. Moderate-sized shells with weakly convex to flat-sided whorls. Distinct adpressed suture, often undulates and is occasionally grooved. Ornament extremely variable in size, strength and pattern, both within the genus and within species; consists basically of tuberculate spiral cords and axial ribs. Adapical ornament frequently prominent and separated from the remainder. Opisthocyrt to opisthocline growth lines. Genus is characterized by the presence of a prominent varix diametrically opposite the aperture on the body whorl. In some species, varices occur on earlier whorls but these are never aligned as in other Cerithiidae. A varix thins towards the adapical and abapical sutures. Small, low, rounded to quadrangular aperture with a short anterior canal and a weakly developed adapical 'gutter', or channel. Smooth, curved columella with callused inner lip; basal lip nearly flat, outer lip not expanded outwards.

Discussion. Cossmann (1906 : 121) considered *Exechocirsus* a subgenus of *Tympanotonus* Schumacher, 1817 on account of some similarity in ornament, but more particularly, because of their apertural characters. However, despite these resemblances it would seem reasonable to reserve the genus *Tympanotonus* for non-marine gastropods and to place the marine *Exechocirsus* in a separate genus.

Exechocirsus also has certain similarities with other Upper Cretaceous and Lower Tertiary cerithiid genera, e.g. *Thericium*, *Clava* (*Clavocerithium*), *Clava* (*Pseudovertagus*), *Serratocerithium* and *Teliostoma*. There is a common element in shell shape, size and in ornament patterns (in many cases varices occur at intervals), while apertural features are also alike. Further studies may show that *Exechocirsus* is a precursor of these genera and probably of other groups of the Cerithiacea such as *Potamides* and even *Cerithium* itself. Certainly, from amongst the few Cretaceous cerithiids, *Exechocirsus* appears to be the most likely ancestor for many of the Tertiary forms and this warrants its consideration as a separate genus. The possession of essentially cerithiid characters suggests inclusion in the sub-family Cerithiinae (Cerithiidae) rather than to accompany *Tympanotonus* in the Potamididae.

Pčelincev (1953 : 192) has attempted to explain the strong and varied ornament occurring within the genus, by suggesting that it probably increased the mechanical stability of the shells and he cites their prolific occurrence at Gosau, in company with thick shelled Opisthobranchs and *Nerinaea*, as evidence.

With regard to the type species of the genus, *Cerithium cingillatum* Zekeli, it is possible that this may be the early whorls of *Cerithium pustulosum* J. de C. Sowerby, 1835, a species which is also recorded from the Upper Cretaceous at the same locality (Gosau, Austria).

Exechocirsus saundersi (Woods)

(Pl. 7, figs 3–5)

1896 *Cerithium saundersi* Woods: 92, pl. 4. figs 12 & 12a.
1921 *Cerithium saundersi* Woods, Ravn: 47.

HOLOTYPE. Sedgwick Museum, B 4459, Cuckhamsley, North Farnborough, Berks., Turonian, Holaster planus Zone.

OTHER MATERIAL. Chalk Rock, G 66724, Latimer, Bucks.; G 69915, Henley Quarry, ? Medmenham, Bucks; GG 20821, GG 20825–20826, Hitch Wood Pit (Hill End Farm), nr. Hitchin, Herts.; G 67704 H. planus Zone Dover; G 11523 Missenden, Herts.; GG 20829, Kensworth Quarry, Beds. Forbes (1960: p. 237) records a large specimen from H. planus Zone, Western Colville, Cambs., SM. B 81559.

DESCRIPTION. Medium-sized, slightly elongate shell with almost flat-sided whorls. Distinct impressed linear suture, which owing to the shell ornament appears to undulate a little. There are four equal spiral cords, with interspaces from one half to equal width between them. These cords are ornamented by rounded tubercles, which are longitudinally aligned, occur at the junctions of the cords and ribs and conform to the orthocline (or very slightly opisthocline) axial ribs. In general, the axial ribs number about sixteen per whorl, but this varies according to growth, and their interspaces are equal to their width. There are a varying number of fine spiral threads between the tuberculated cords. In some specimens, a smooth partly undulating cord occurs below the main spiral and just adapical to the suture. Woods had described and figured this, but in the holotype this cord appears to be composed of much smaller and more numerous tubercles (see pl. 7, fig. 5).

The base is flat to very slightly convex, has a sixth granular, sub-carinate cord near the border and numerous spiral threads crossing its surface. The aperture is only partially exposed but appears to be obovate to quadrangular. It shows a short, well-formed anterior canal that is slightly curved, a callused inner lip and a concave columella. A strong varix occurs opposite the aperture on the last whorl and in a few specimens, there are indications of others on earlier whorls.

Discussion. The occurrence of a strong varix on the last whorl diametrically opposite the aperture is characteristic of the genus *Exechocirsus.* In his original description, Woods distinguished the new species from *C. pustulosum*, J. de C. Sowerby (1835: pl. 39, fig. 19) by its smaller spiral angle and fewer tubercles. Another feature is that the axial ribs are more definite; they are also opisthocyrt and only incorporate the tubercles of the lower three cords, those on the adapical cord remaining unconnected. The tubercles on the abapical cord become somewhat elliptical and on successive whorls they gradually diminish in size (see Zekeli, 1852, pl. 19, fig. 5). Finally, there are undoubtedly more longitudinal rows of tubercles, i.e. ribs, per whorl, in *E. pustulosum* (J. de C. Sowerby).

Cerithium pustulosum d'Orbigny (non Sowerby), 1843 resembles *E. saundersi* in ornament, but its longitudinal rows of tubercles are strongly opisthocline and are also said to be farther apart (Zekeli, 1852 : 100). In addition, the suture is grooved and the aperture more ovate.

Woods also separated *E. saundersi* from *C. pseudoclathratum* d'Orbigny, 1850 (as figured in Geinitz, 1874, pl. 31, fig. 5), yet, although the latter has similar ornament, its true generic position is uncertain. Sohl (1960 : 83) included *C. pseudoclathratum* with two American, Upper Cretaceous species that he has since (1964 : 364), mentioned as being closely related to *Cerithiella* Verrill, 1882.

The Upper Cretaceous, *Cerithium navasi* Vidal, 1917 from Sensui, Spain, is easily distinguished from *E. saundersi*, in only having three tuberculate spiral cords and a less prominent, finely-beaded, cord at the abapical suture.

It is difficult to decide the relationship of several British specimens which show slight differences from typical *saundersi* ornament, owing to the lack of knowledge of the range of ornament variation occurring in that species. In a number of these examples, the tubercles appear to be more numerous and this obscures any regular axial alignment that they may have.

Two undescribed, unlocalized specimens from the Sowerby Collection G 60542–60543, and others in material collected by C. W. Wright from Hitch Wood Pit, Hitchin, Herts. (GG 20822–20824) show distinctive features (see pl. 7, figs 8 & 9; 1, 2 & 12). Basically there is a stronger development of both primary and secondary spiral cords, while the axial ribs are fewer (12–14 per whorl) and consequently wider apart. Among other features, the adapical cord is separated from the others by a much wider interspace, the suture occurs in a groove formed between adjoining whorls and varices frequently occur on earlier whorls.

In BM(NH) G 67704, (pl. 7, fig. 4) from the Chalk Rock of Dover, some of the very earliest whorls are preserved. Initially, the whorls are ornamented by two tuberculate spiral cords, this eventually increases to three and within a further two whorls, to four. The spire in this specimen is considerably more slender than those of other species included in *Exechocirsus*. In another specimen, BM(NH) GG 20821, pl. 7, fig. 1) the tubercles are weakly developed but the axial ribs produce a rather longitudinal step-like appearance in the shell, which also has a more distinctive suture.

Other material BM(NH) GG 5932–5934, GG 5982–5983, GG 5987 and GG 5771 (see pl. 7, figs 13 & 14) collected by C. W. Wright, from the Holaster planus Zone at Kiplingcotes in East Yorkshire, is obviously related to *E. saundersi*. The slender shape of the shells, their markedly opisthocyrt growth lines and opisthocyrt (rather than opisthocline) ribs suggest they are a different form. Additional support to such a view, is provided by their intermediate spiral threads, which are stronger than in typical *saundersi* and by the fact, that in general, they are much smaller specimens. It is possible that these features are the result of a phenotypic response to differences in environment and for the moment, the specimens are regarded as *Exechocirsus* aff. *saundersi* (Woods).

? ***Exechocirsus*** aff. ***subpustulosus*** Pčhelincev, 1953

(Pl. 7, figs 10 & 11)

1953 *Tympanotonus* (*Exechocirsus*) *subpustulosus* Pčhelincev: 193–194, pl. 33, figs 13–16.
1960 *Tympanotonos* (*Exechocirsus*) *subpustulosus* Pčhelincev, in Orlov, pl. 19, fig. 13.

Material. BM(NH) G 73798 and G 16134, Upper Greensand, Upper Albian, Haldon, Devon.

Description. Poorly preserved medium-sized turriculate shells with feebly convex whorls that have a very small adapical sutural ramp, a slightly grooved undulating suture and opisthocyrt growth lines.

The whorls are ornamented by about 18 narrow axial ribs, that are orthocline on the early whorls but rapidly become opisthocyrt. These ribs are separated by interspaces that are at least equal to their width. On the earlier whorls a narrow spiral groove cuts the ribs to produce an adapical row of tubercles. Other similar spiral furrows occur abapically to this, on later whorls, and these dissect the ribs even more, with the result that the original predominantly axial ornament becomes changed to a spiral pattern. A single spiral thread occurs in each groove. Numerous fine spiral threads can be seen in the interspaces between the ribs. Further spiral grooves occur towards the base on the last whorl. Neither the base of the shell or the aperture can be seen.

Discussion. Lacking knowledge of apertural details and without any indication that these specimens possess the characteristic varix of *Exechocirsus*, it is not possible to refer them to that genus with certainty. They are provisionally referred to the Transcaucasian Cenomanian *Exechocirsus subpustulosus* Pčhelincev (1953) on the basis of ornament resemblance. The axial ribs of *subpustulosus* are also dissected by spirals to produce four rows of tubercles and both species have a rounded base.

Although the adapical rows of tubercles is the most prominent and is also separated by a wide groove from the lower rows, it has fewer tubercles than that of the British specimens. Pčhelincev remarked that there is a tendency for the ornament of *subpustulosus* to become weaker on later whorls and this effect is also apparent in the Haldon material. It is only the lack of varices on the earlier whorls, together with the narrow apical angle, that enabled Pčhelincev to distinguish his species from *E. pustulosus* (J. de C. Sowerby).

Family ? **CERITHIIDAE**

Genus ***AGERIA*** nov.

Named in honour of Dr D. V. Ager, Professor of Geology at the University of Swansea, in recognition of his help and advice.

TYPE SPECIES. *Ageria gaultina* sp. nov.

DIAGNOSIS. Turriculate shells, ornamented by spiral cords and axial ribs; the cords are frequently beaded and the abapical cord is characteristically strongly developed and ornamented.

GENERIC CHARACTERS. Small-medium sized, slender, turriculate shells. Convex whorls with a slight concavity before an abapical astragal. Flush, slightly grooved, undulating suture. Regular ornament formed by axial ribs and spiral cords. In some species the axial ribs weaken on later whorls, but in all species they have a characteristic opisthocyrt shape. In most species, the primary spiral cords are beaded, but in some the cords are smooth. A strong cord forms a distinctive abapical feature which delimits the base. Opisthocline growth lines influence the spiral ornament and show a median sinus, they swing back towards the columella on the uniform basal slope. Axially elongate, quadrangular aperture and indication of a short anterior canal with a smooth, slightly curved columella.

DISCUSSION. The general shell shape and ornament, together with the slight indication of a short anterior canal, suggest that this distinctive group should be included in the Cerithiidae. Yet, the lack of adequately preserved material showing the aperture prevents a definite conclusion being formed; particularly as the indications of an anterior canal in the type species *A. gaultina* sp. nov., could be the result of crushing. Consequently, it is not possible to assign *Ageria* to a particular subfamily of the Cerithiidae. Furthermore, its similarity in ornament to the procerithiid genus *Cryptaulax* Tate, 1869 is noticeable and the possibility that *Ageria* could be derived from this cannot be dismissed.

In many respects, the generic characters resemble those found in members of the Turritellidae, i.e. the turreted shell, the whorl outline and the possession of a thin parietal lip with a smooth columella. However, the holostomous, sub-circular aperture of the Turritellidae makes any further comparison rather pointless, while the characteristic lack of axial ornament in that family together with the marked sinuosity of its growth lines and outer lip and the deeply excavate columella provide further distinguishing characters.

Two species that can now be referred to *Ageria* are *Turritella costata* J. de C.

Sowerby, 1827, Upper Greensand, Albian, Blackdown, Devon; and *Cerithium binodosum* Roemer in Frič (1894, text-fig. 87), Lower Senonian, Březno Beds (= Priesener Schichten) Březno, Czechoslovakia.

Questionably referred species are *Turritella angustata* d'Orbigny, 1850 from the Neocomian of France (see p. 158) and *Cerithium hector* d'Orb. (1850, p. 156) in Guéranger, 1867 (pl. 14, fig. 2), Cenomanian from Le Mans, France.

The original figure of *Turritella cingulatolineata* J. Müller (1851, p. 33, figured as *cingulatocostata*, pl. 6, fig. 15) from Aachen appears to be that of an *Ageria*, having a characteristic prominent abapical cord. Yet, the ornament shown in the figure provided by Holzapfel (1888, pl. 14, fig. 1) when he interpreted Müller's species as belonging to the genus *Mesostoma*, is quite unlike that of *Ageria*. This figure shows a median row of prominent tubercles, while its quadrangular aperture hints at the presence of a strong abapical cord.

Ageria gaultina sp. nov.

(Pl. 8, figs 1–5)

DIAGNOSIS. Narrow, turriculate shell, ornamented by orthocline axial ribs which do not persist on later whorls; its strong abapical cord is carinate.

HOLOTYPE. BM(NH) GG 6473 Albian, Gault, Folkestone, Kent. J. S. Gardner Collection.

OTHER MATERIAL. BM(NH) G 4362 (26 specimens), G 11318, G 11544, G 20741–20742, GG 20857–20862, 38085 (2), 48136 (3), Albian, Gault, Folkestone. G 71026, Gault, East Wear Bay, nr. Folkestone, Kent and G 49804, Albian, Osmington, Dorset.

Dr H. G. Owen of the Dept. of Palaeontology, BM(NH) considers that the matrix of GG 20742 is consistent with that of Bed V of the Lower Gault at Folkestone, in the Lautus-Nitidus Subzone.

DESCRIPTION. Small to medium-sized, turriculate shell, with an acute spire composed of moderately high whorls (height equal to $\frac{3}{4}$ of width). Flush, linear suture. Whorl outline slightly convex but briefly becoming concave before an abapical peripheral carina.

Whorls ornamented by nine orthocline axial ribs, that are crossed by numerous beaded spiral cords (22 from adapical suture to the peripheral carina in the holotype), with the interspaces separating the ribs equal to twice the width of a rib. These axial ribs are successively displaced from whorl to whorl and this produces a counter spiral pattern in relation to the direction of coiling (see pl. 8).

Such ornament occurs in the earliest whorls, but initially the orthocline ribs are much stronger than the simple spiral cords and therefore, in cross section, the whorls are angular. The basal beaded spiral is the first to become differentiated with other cords soon developing and varying in strength and composition. A pattern of five strongly beaded primary cords with a varying number of more finely beaded secondary cords occurring in their interspaces is formed. In some cords the beads are rounded, in others they become elongated in the direction of the growth lines, while the 'beads' of some secondary cords are the result of the growth lines simply dissecting the cord. As the ornament of the spirals strengthens, the ribs tend to diminish and are almost obsolete on later whorls, where they are only indicated by the presence of strong tubercles on the primary cords. The opisthocline growth lines influence the spiral cords, but do not affect the direction of the axial ribs.

The base is delimited by the prominent basal spiral cord and this is followed inwards by a second, less prominent, primary cord, the base then slopes uniformly to the columella. The remainder of the surface is ornamented by alternating granulose spiral cords and smooth spiral threads. After crossing the basal carina, the growth lines swing sharply back towards the columella.

Unfortunately, a completely preserved aperture is not available, but it is probably somewhat quadrangular and axially elongate. There are some indications of a short anterior canal but this may have resulted from crushing of the shell. The outer lip is virtually straight in cross section, but the growth lines show a slight median sinus. The inner lip is smooth, partly callused and rather narrow. The columella is very slightly curved, but this could also be a result of crushing.

Discussion. There is a little variation within the ornament of this species. A specimen of 5 whorls, found at Osmington, Dorset, BM(NH) G 49804 (see pl. 8, fig. 5) has only thirteen spiral cords between the adapical suture and the basal carina and not one of these cords is beaded, yet it does show a typical sequence of primary cords. Among ornament variations shown by material collected from the Gault of Folkestone, Kent are more equidistant primary cords; a less prominent peripheral beaded carina; broader (i.e. thicker) spiral cords ornamenting the base and a considerable range of differences in the strength and dominance of both spiral and axial elements on the early whorls (see pl. 8, figs 2, 3, 4 & 6, BM(NH) GG 20741–20742, GG 20857, GG 20862).

Ageria gaultina is easily distinguished from *A. costata* (J. de C. Sowerby), described below, by its orthocline axial ribs and the fact that these ribs do not persist on to later whorls. Its more carinate abapical cord also serves to identify the species.

The specimen figured as *Cerithium binodosum* Roemer, by Frič (1894, text-fig. 87), from the Lower Senonian, Březno Beds (Priesener Schichten) of Selten, nr. Louny, N. W. Bohemia, Czechoslovakia, is not like any other specimen figured as *C. binodosum* Roemer, 1841 and undoubtedly belongs to the genus *Ageria*. It possesses the distinctive, strongly ornamented abapical spiral cord of that genus and has very similar whorl and apertural shapes. The cancellate pattern formed by its axial ribs and spiral cords separates it from other species of *Ageria*.

Cryptaulax angustatum (d'Orbigny), Peron (1900 : 93, pl. 1, fig. 14) from the Neocomian of France, is probably another species of *Ageria*. The ornament, whorl shape, axially elongated quadrangular aperture, and smooth, slightly curved columella, are features in common with other members of that genus. Yet, its aligned (initially orthocline) prosocline axial ribs are also strongly reminiscent of the genus *Cryptaulax* Tate, 1869. The apparent lack of a strong abapical cord adds to the uncertainty, while its smooth spiral cords would readily distinguish it from the recognized species of *Ageria*. All of these features are discernible in the figures provided by both d'Orbigny (1842, pl. 151, figs 4 & 6) and Peron, and in a British Neocomian specimen BM(NH) GG 20740, from the Claxby Beds, Nettleton, Lincs. (see pl. 8, fig. 13).

Ageria costata (J. de C. Sowerby)

(Pl. 8, figs 7–12)

1827 *Turritella costata* J. de C. Sowerby: 126, pl. 565, fig. 4.
1900 *Turritella costata* Sow., Jukes-Browne: 464.

DIAGNOSIS. Acicular shell with persistent prosocline axial ribs and a shelf-like abapical cord.

HOLOTYPE. BM(NH) 43674, Albian, Upper Greensand, Blackdown, Devon, Sowerby Collection.

OTHER MATERIAL. BM(NH) 34844 (2 specimens), G 20830–20832, G 71382, G 16142 (2 specimens) from Upper Greensand, Blackdown, Devon; G 71090–71095, from Bed 12 Peak Hill, nr. Sidmouth, Devon, H. F. Metcalfe Collection.

DESCRIPTION. A small, slender, somewhat subulate shell with convex whorls that appear to be twice their height in width. Flush, undulating suture occurs in a very slight groove beneath the abapical astragal. The whorl outline becomes concave just before this astragal and causes a small constriction in its shape. The growth lines are opisthocline and show a definite median sinus.

The shell is characteristically ornamented by a consistent pattern of axial ribs and spiral cords. Initially, the eight, or ten ribs are orthocline and dominate the ornament. However, the ribs soon become prosocline and terminate above the basal astragal as described by Sowerby. The spiral ornament consists of four to five beaded to tuberculate primary cords with both weaker beaded cords and smooth threads between these. The peripheral carina, or astragal, is shelf-like and dissected by numerous growth lines. The flattish base is ornamented by rather broader spiral cords than those of the whorl side. A strong cord, just in from the carina, forms the main feature.

The aperture (see pl. 8, fig. 9) is quadrangular and elongated axially, with a notch in the outer lip just above the astragal. The parietal lip is quite thin and the columella is not callused. The base of the aperture is flat and an anterior canal is not apparent.

DISCUSSION. Although this species is very similar to *Ageria gaultina* sp. nov. in ornament, there are a number of differences between them. The orientation of its axial ribs is markedly prosocline as opposed to the orthocline ribs of *gaultina*. A further contrast is that in *costata* the ribs persist and occur on later whorls. The shell also appears to be more needle-like in shape, even though its whorl diameter: whorl height ratio seems lower than that of *A. gaultina*. The whorls of *costata* are more convex, while the abapical astragal that delimits the base of the two species, is shelf-like in *costata* and carinate in *gaultina*.

Family **CERITHIOPSIDAE**

Genus ***CERITHIELLA*** Verrill, 1882

[*Lovenella* Sars, 1878, non Hincks, 1869; *Newtonia* Cossmann, 1892, non Schlegel, 1866; *Newtoniella* Cossmann, 1893; *Cerithiolinum* Locard, 1903].

Type by original designation, *Cerithium metula*, Lovèn, 1846, Recent.

REMARKS. Wrigley (1940 : 13) considered that *Cerithiella* has a moderately deep sunken suture and that its subordinate axial riblets cross the spiral carinae frequently producing nodes at the intersections. In his view, the related genus *Seila* has an inconspicuous suture, is composed of essentially flat-sided whorls and its fine axial threads are only visible in the interspaces between the spirals. However, in instances where species have ornamental features similar to those of *Seila*, the truncate concave columella and short twisted anterior canal of *Cerithiella* is easily distinguishable from the virtually straight columella occurring in *Seila*. The aperture of *Cerithiella* has been described as sub-quadrangular as opposed to the sub-ovate shape found in *Seila*.

The Cretaceous species mentioned in the discussion below, were originally assigned to the genus by Sohl (1964 : 364).

Cerithiella (Cerithiella) devonica sp. nov.

(Pl. 6, fig. 9)

MATERIAL. Unique specimen in the Sedgwick Museum, Cambridge, B 44633 from the Upper Albian, Blackdown, Devon.

DIAGNOSIS. Acuminate cerithiopsid with cancellate ornament consisting of three equally-spaced tuberculate spiral ribbons and numerous fine axial threads and possessing a short twisted anterior canal.

DIMENSIONS. Height = 11 mm; Maximum diameter 3 mm.

DESCRIPTION. Small slender shell with turriculate spire. Whorls almost flat-sided and with a very slight adapical ramp. Linear suture in moderately-deep asymmetric channel formed by adjacent whorls. Ornament consists of three equally-spaced spiral ribbons, the adapical ribbon being very slightly weaker. Very faint spiral threads occur on the short ramp below the adapical suture. The concave interspaces are equal to the width of the spirals. The fine axial threads are slightly opisthocline and produce angular tubercles where they cross the spiral ribbons. Ornament of the thirteen preserved whorls is consistent. The basal ornament, growth lines and protoconch are not adequately preserved for description. The aperture is incomplete but there are indications of a short twisted anterior canal.

DISCUSSION. The characters of ornament, whorl shape, suture and aperture appear to be sufficient to indicate that this specimen belongs to the genus *Cerithiella*. Its cancellate ornament of three spirals and numerous axial threads is very close to that of the North American Upper Cretaceous species *C. nodoliratum* (Wade), 1926. On comparison with the figures given by Sohl (1960; pl. 9, figs 15–16, 24) only a slightly longer anterior canal in *nodoliratum* and the presence of the fine spirals on the short adapical ramp of *devonica* could be used as distinguishing features. Yet, these small differences when considered together with the widely separate geographical and stratigraphical occurrence of the two forms would seem to support the belief that they are distinct species. Unfortunately, the basal ornament of the British specimen is not preserved and consequently, it is not possible to verify the distinctive growth line pattern on the base of the shell, described by Sohl (1964 : 365) for the American cerithiopsids.

C. semirugatum (Wade) 1926 and *Cerithiella* sp. nov. Sohl, 1964 are easily distinguished from *C. devonica* by their ornament of four spiral ribbons. Similarly, the ornament of four variable cords in *Cerithium bicostatum* Kaunhowen (1898 : pl. 6, fig. 17) from the Maastrichtian of Belgium, separates that species from *devonica*. Kaunhowen also mentions a short, but straight canal, in his description.

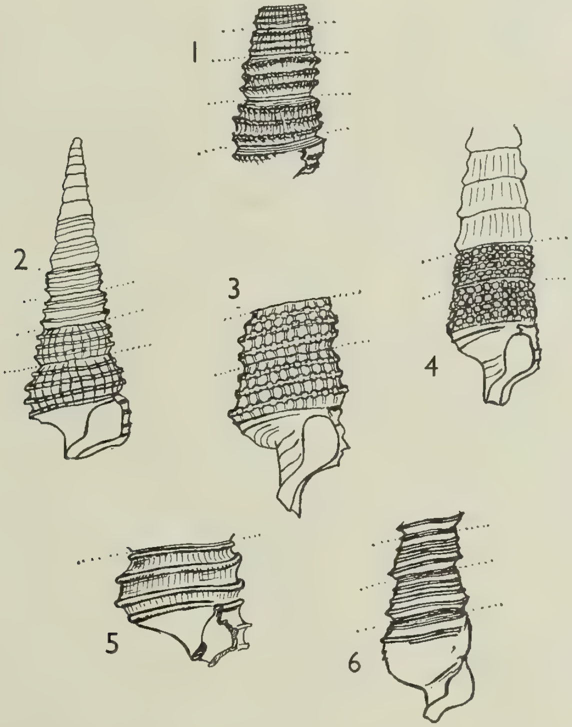

FIG. 2. 1, *Cerithiella devonica* sp. nov., Cretaceous, Upper Greensand, Albian, Blackdown. Devon. ×4. *Cerithiella metula* (Lovèn). Type species. Recent, North Sea. ×2·6. 3, *Cerithiella nodoliratum* Wade, Cretaceous, Maastrichtian, Ripley Formation. Tennessee, U.S.A. ×5. 4, *Cerithiella semirugatum* Wade, Cretaceous, Maastr., Ripley Formation, Tennessee. U.S.A. ×4·6. 5, *Cerithiella cloacina* Wrigley, Eocene, London Clay, Whitton, Middx., England. ×5. 6, *Cerithiella atherfieldensis* sp. nov., Cretaceous, Lower Greensand, Aptian, Atherfield, Isle of Wight. ×2.

The more turreted character of the Lower Aptian, *Cerithiella atherfieldensis* sp. nov. described below, together with the variation in strength of its spiral cords, its sub-carinate whorls and limited axial ornament provide distinguishing characters. In some Tertiary examples of the genus, *C. cloacina* Wrigley and *C. praelonga* (Deshayes) the spiral cords are smooth. [Text-fig. 2]

Cerithiella (Cerithiella) atherfieldensis sp. nov.

(Pl. 6, fig. 10)

HOLOTYPE. Sedgwick Museum, Cambridge B 27334 from the Lower Aptian, Forbesi Zone, Crackers, Lower Greensand, Atherfield, Isle of Wight.

DIAGNOSIS. Narrow, turreted shell, ornamented by five spiral cords of varying strength (the fourth producing a slight carination before the grooved suture) and limited axial threads.

DESCRIPTION. Small, acutely spiral turreted shell of slightly convex, sub-carinate whorls. Distinct suture in narrow groove. Protoconch not preserved. Aperture sub-ovate with a strongly twisted anterior canal; short truncated columella. Shell ornamented by five, more or less equidistant primary spiral cords and fine axial threads. A cord occurs on either side of the suture with three stronger ones in the centre of the whorl. The more abapical of these is the strongest and almost forms a carina. The interspaces are much wider than the width of the cords and a fine secondary spiral cord occurs in each of the two central interspaces. On the base, a prominent interspace separates numerous fine spiral cords from the most abapical primary cord. The fine axial threads are slightly opisthocyrt on the whorl side and are not visible on the base. These axial threads are more prominent on the earlier whorls but always weaker than the spiral cords.

DISCUSSION. In this species, the small spiral angle, the limited axial ornament, the somewhat turreted appearance, the variation in strength of its spiral cords, and the abapical carination of the whorls, all serve to distinguish *C. atherfieldensis* from the other Cretaceous species mentioned in the discussion of *C. devonica*. It is also the earliest recorded species of this genus.

Genus ***SEILA*** Adams, 1861

[*Cinctella* Monterosato, 1884]

Type by subsequent designation, Dall (1889 : 250), *Triphoris dextroversus* Adams & Reeve, 1848, Recent.

DIAGNOSIS. (After Sohl, 1960 : 84 and 1964 : 364). Moderately small to very small, slender, turriculate, thin shell. Smooth, swollen, paucispiral protoconch. Whorls flat-sided and ornamented by prominent, smooth spiral, ribbon-like cords with numerous fine growth-line threads in their interspaces. Indistinct suture. Last whorl moderately high and with a carina at basal periphery. Aperture subovate, short anterior canal with a swelling on base of almost straight columellar lip. Outer lip thin.

Seila iglali sp. nov.

(Pl. 6, fig. 11)

Material. Unique specimen, BM(NH) G 16084, from the Upper Greensand, Albian, Combe Raleigh Hill, nr. Honiton, Devon, W. Vicary Collection.

Diagnosis. Conical shell, large for genus, ornamented by four raised, flat-topped spiral ribbons on whorl side and numerous smooth spiral cords on base, with transverse threads occurring in the interspaces.

Description. Small, conical shell (Height: 13·5 mm; Maximum diameter: 4·8 mm) with a flat-sided whorl outline. Whorls ornamented by raised, flat-topped spiral cords (i.e. 'ribbons') with fine transverse threads in the concave interspaces between these. Distinct linear suture occurs in a symmetrical groove between adjacent whorls.

Early whorls appear to be smooth and rather convex (although this may be the result of poor preservation). Traces of axial ornament can be seen adapically on the fourth whorl, while the fifth shows faintly the typical ornament of subsequent whorls. This consists of four prominent flat spiral ribbons that are approximately equal in width but vary in their distance apart (see Text-fig. 5). The fourth ribbon is slightly narrower and forms a basal carina. The concave interspaces are crossed by regularly-spaced, easily visible, axial threads. Interspaces roughly three times the width of a thread. Axial threads essentially orthocline, but towards the base, i.e. between the third and fourth spiral ribbons, and particularly on later whorls, they tend to become opisthocline. On close examination, it is possible to see that the axial threads cross over the spiral ribbons.

Within the basal carina, and after a further concave interspace, the flat surface of the base is ornamented by numerous (15–16) identical smooth spiral cords that continue on to the columella and are separated by intervals equal to their width. Growth lines are not visible on the base.

Aperture small and sub-ovate; columella broad and equal to one third of the whorl diameter, and is twisted anteriorly. Anterior canal short and narrow.

Discussion. The general flat whorl outline, together with its ornament of raised, ribbon-like spirals, leads one to consider this species as a member of the genus *Seila*. However, its size, which is greater than that of most species assigned to this genus, and its distinct linear suture, cause some uncertainty. In addition to these doubtful features, its conical shell shape is also rather unusual and quite unlike the slender, sub-cylindrical form of the type species *Seila dextroversa* (Adams & Reeve). In a number of Recent species of the genus, the base of the anterior canal forms a slit, which extends for one third of the whorl's circumference. This feature is certainly lacking in *S. iglali* and while this could be due to poor preservation, it also appears to be lacking in North American Upper Cretaceous species which suggests that it is not present in these earlier forms. Obviously, in order to confirm that this Albian fossil is correctly assigned to the genus *Seila*, it is necessary to obtain a well-preserved protoconch.

Sohl (1960 : 84) refers the North American, Upper Cretaceous species *Cerithiopsis* *meeki* (Wade, 1926) and *Cerithiopsis quadrilirata* (Wade, 1926) found in the Ripley Formation (Maestrichtian), to the genus *Seila*, on the basis of their ornament and protoconch features. Since the columella fold found in both of these species is much stronger than in typical *Seila*, and, in fact, more reminiscent of other Cerithiopsidae, he qualifies this decision. Yet, as none of these genera possess ornament similar to that of *meeki* and *quadrilirata*, he refers the two species to *Seila*.

Seila iglali is very close to *S. meeki* (Wade) and apart from their considerable difference in size, the only feature that will separate the two species is the presence of a fourth spiral ribbon in *iglali*. In both *Seila quadrilirata* (Wade) and *Seila* sp. Sohl, (1960 : 85, pl. 9, fig. 23), some of the spiral ribbons are very close together. Among other distinguishing features, the axial threads of *S. quadrilirata* are finer and more numerous and also described as being prosocline; while in *Seila* sp. no. axial threads are present. Sohl (1964 : 364) has also recorded *S. meeki* from a slightly older horizon in the Upper Cretaceous [Coffee Sands of Mississippi (Campanian)] and noted that its spiral ribbons were much thinner and consequently farther apart. The limited amount of material available, prevented him from considering the possible significance in this.

Among Eocene species, *Seila mundula* (Deshayes, 1865 : 222) is the closest to *iglali*, but can be separated by its convex base and very much finer axial threads. In contrast, to the Cretaceous specimens referred to ?*Cerithiella*, there is no indication of secondary spirals developing in the interspaces of the primary ribbons in *S. iglali*.

If the determination of this specimen is correct, it will be the earliest record of the genus.

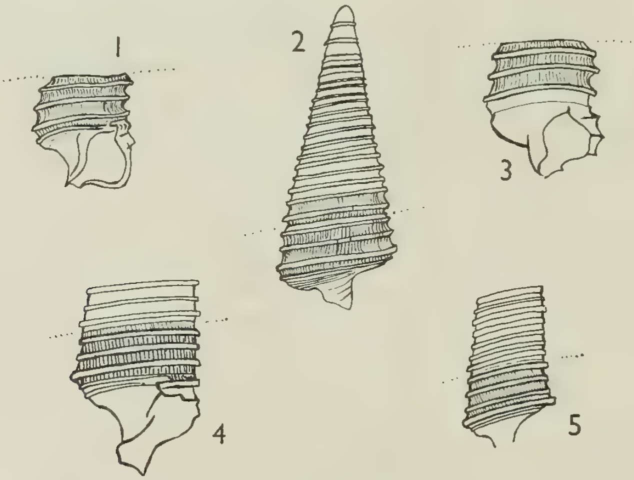

FIG. 3. 1, *Seila dextroversa* (Adams & Reeve), type species of genus. Recent. China Seas. ×9. 2, *Seila iglali* sp. nov., Cretaceous, Albian, Devon, England. ×2·6. 3, *Seila mundula* (Deshayes), Eocene, London Clay. Highgate. ×3·3. 4, *Seila meeki* (Wade), Cretaceous, Maastrichtian. U.S.A. ×5 approx. 5, *Seila quadrilirata* (Wade) Cretaceous, Maastrichtian, U.S.A. ×3·3 approx.

Genus ***ORTHOCHETUS*** Cossmann, 1889

Type species. By original designation, *Cerithium leufroyi* Michelin in Deshayes, (1833 : 380), Lutetian, France.

Diagnosis. (After Wenz, 1940 : 779). Medium-sized, slender, turriculate regularly conical shell, composed of numerous low whorls that have an abapical keel. Whorls ornamented by spiral cords and axial riblets, frequently producing a reticulate network. Last whorl approximately one third of shell height. Aperture subquadrangular, with a strong, moderately long, truncated canal; thin outer wall, slightly sinuous adapically. Columella straight, with base a little twisted; may be smooth, or with several oblique folds. Growth lines opisthocline to opisthocyrt, but swing back towards the columella on the base.

Orthochetus hantoniensis sp. nov.

(Pl. 6, fig. 12)

Material. BM(NH) G 70130, Aptian, Atherfield, Isle of Wight.

Diagnosis. Slender, turreted cerithiopsid with an abapical carina and strongly developed axial ribs (fewer in number than normal), which influence five of the six spiral cords to produce a frilled appearance. Columella straight, but uncharacteristically short and apparently without plications.

Description. Small, slender, turreted shell with fairly low whorls. The suture is subcarinate and linear, but axial ribs may give it an undulate appearance. The protoconch is not completely preserved, but early ornament seems to be identical to that of later whorls. This ornament consists of strong, straight axial ribs (15–16 per whorl) that are separated by interspaces equal to their width; and six spiral cords of varying strength. A slight adapical ramp occurs immediately beneath the suture and this is bounded by a strong spiral cord. At equal distances below this follows a very weak cord, a moderately strong cord, then at the abapical carina another strong cord, and, finally, another weak cord.

All of these five cords are influenced by the axial ribs, the apparent thickening at their intersections producing a frilled, or tuberculate appearance to the shell. A sixth spiral cord close to the abapical suture, limits the base and is unaffected by the axial ribs. The axial ribs diminish soon after the abapical carina.

Numerous faint opisthocline growth lines occur on the whorl side and on the base these swing back towards the columella. Columella moderately short and straight with faint oblique ornament along its length. Small aperture subquadrangular, showing a well-developed, twisted and truncated anterior canal. Thin sinuous outer lip.

Discussion. The distinctive ornament and slender turreted spire of this species, together with its general apertural features, are sufficient to refer it to the genus *Orthochetus*. However, the columella is somewhat shorter than is usual, while its twisted anterior canal is less inclined; in fact, such features are reminiscent of the genus *Cerithiella*. The strongly developed axial ornament and its consequent influence on the shell's appearance are adequate diagnostic features to separate this species from others that have been described. The lack of plications on the columella might be construed as uncharacteristic of *Orthochetus*, yet, Wrigley (1940 : 11 & 12) mentioned a number of instances in Eocene species where this feature is obscured by a reflected columella border.

Its diagnostic features distinguish *O. hantoniensis* from the two Maastrichtian species mentioned by Cossmann (1906 : 97) *Cerithium tectiforme* Binkhorst (1861: 24 pl. 1 figs 3a–c) from Limbourg and *O. mapeulensis* Douvillé (1904 : 303 pl. 41 fig. 12) from Kouh Mapeul, Persia. The ornament of both these Maastrichtian species is more reticulate, due to the presence of smaller and more numerous axial ribs. Although both *O. hantoniensis* and *O. tectiformis* have three primary spiral cords, the presence of secondary spirals in the former and of tubercles in the latter assist in separating the two species.

Douvillé (1904 : 303) referred to *Orthochetus* as an ancient group and quoted the occurrence in the Chalk of *Cerithium cribriforme* Zekeli (1852 : pl. 20, figs 2 & 2′) as evidence. In many respects, this turreted species is very like *O. hantoniensis*,

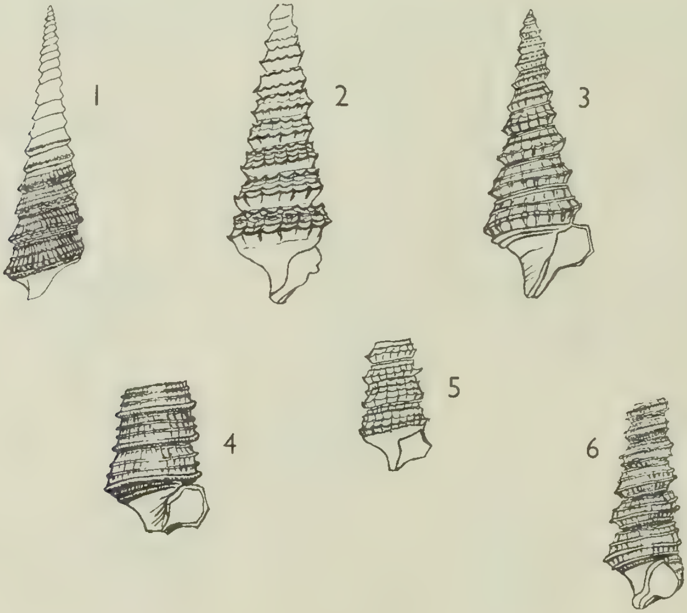

FIG. 4. 1, *Orthochetus tectiformis* (Binkhorst), Cretaceous, (Maastrichtian), Limbourg Netherlands. ×1·3. 2, *Orthochetus hantoniensis* sp. nov., Cretaceous (Aptian). Atherfield, Isle of Wight. ×3·3. 3, *Orthochetus leufroyi*; (Michelin in Deshayes 1833). Eocene. Chaumont, France. Type species. ×0·6. 4, *Orthochetus charlesworthi* (Prestwich), Eocene, London Clay. Sheppey, Kent. ×0·6. 5, *Orthochetus mapeulensis* Douville. Cretaceous, (Maastrichtian). Louristan, S. Persia. ×1·3. 6, *Orthochetus elongatus* Wrigley. Eocene, London Clay, Sheppey. ×0·6.

having strong axial ribs and three smooth spiral cords undulating over them. Yet its aperture is not shown, and there are no indications of secondary spirals in the figure which does show that *C. cribriforme* is rather awl-shaped, i.e. subulate. The existence of *O. hantoniensis* would appear to substantiate Douville's claim that the genus *Orthochetus* arose in the Cretaceous, even if *C. cribriforme* Zekeli should prove to be mis-identified.

Several of the larger Eocene species show that the anterior canal and the columella are not necessarily identical to, or as long as that of the type species *O. leufroyi*. Comparison of *O. charlesworthi* (Prestwich) and *O. elongatus* Wrigley illustrates that there is considerable variation in spiral angle and whorl diameter. Wrigley (1940 : 12) also showed that within a species there is a wide variation in the strength and position of its ornament components, e.g. see his figures of *O. elongatus* (p. 17, figs 13–15).

Incertae sedis

? '***Orthochetus***' ***helmyi*** sp. nov.

(Pl. 6, figs 13 & 14)

MATERIAL. BM(NH) G 10500 and G 71988 from the Gault, Albian of Folkestone, Kent.

DIAGNOSIS. Turreted, conical cerithiopsid, ornamented by four prominent flat-topped ribbon-like spiral cords and numerous fine opisthocyrt axial threads.

DESCRIPTION. Medium-sized, slightly turreted, conical shell. Distinct linear suture lies in a furrow between the abapical and adapical primary spiral cords of adjacent whorls. Protoconch not preserved.

Whorl side ornamented by four strong, prominent, flat, ribbon-like spiral cords, with a fifth weaker primary cord occurring at the abapical suture and delimiting the base. The two lower ribbons, i.e. the third and fourth abapically, are stronger and wider. Secondary spiral threads occur in the unequal interspaces between the primary ribbons, but can only be seen easily on the lower halves of later whorls. Fine axial growth threads occur in the interspaces and also continue over the spiral ribbons. These opisthocyrt threads show a broad shallow sinus, which has its apex at mid-whorl; each thread is separated from its neighbour by a space equal to double the width of a thread.

The base is flat to feebly convex and within the delimiting fifth primary cord, it is ornamented by numerous thin secondary spirals. The opisthocyrt growth lines, after crossing on to the base, tend to straighten and then swing back towards the columella. The aperture is sub-quadrangular and has a flat basal lip. The short columella is smooth.

DISCUSSION. It is difficult to assign this species to one particular genus of the Cerithiopsidae without having a specimen that shows the important details of its aperture and protoconch, for its ornament and whorl shape have characteristics similar to those of *Cerithiella*, *Seila* and *Orthochetus*. Reference to the literature and to collections of Tertiary representatives of these genera does not provide any useful guide, since it is apparent that there is some confusion in distinguishing the genera and in assigning species to them. The criteria that Wrigley (1940 : 13) used, have been referred to under *Cerithiella* (page 160), but these are often inadequate, e.g. the inconspicuous suture that is considered a diagnostic feature of the genus *Seila*. Undoubtedly, a reappraisal of the criteria used to distinguish the genera of the Cerithiopsidae is necessary and the review of species assignations suggested by Sohl could be undertaken at the same time.

Some of the features present in '*helmyi*', i.e. the distinct linear suture and the crossing of the spirals by the axial threads, indicate possible affinities with *Cerithiella*. The moderate size of the specimen and the fact that its whorls could hardly be described as flat-sided, indicate that it should not be assigned to *Seila*, but could easily be recognized as a possible member of *Orthochetus*. The presence of prominent, ribbon-like spiral cords and the fine axial opisthocyrt threads and the basal features of the whorl, together with the indications of a short straight columella are reminiscent of several species of *Seila*, including the type species *S. dextroversa*. However, these features could equally be those of *Orthochetus* and therefore after recognizing that the linear suture is very like that of Eocene species of this genus, *helmyi* is provisionally placed in *Orthochetus*. In the majority of described species of this genus, and particularly in the earliest member *O. hantoniensis*, the axial ornament is quite prominent and contributes to the typical reticulate ornament pattern. The size, ribbon-like spirals, super-imposed axial ribs and turreted whorl shape of *helmyi* are considered to be the most important indicators of its probable relationship with *Orthochetus*.

Similar difficulties prevent the assignation of a unique specimen, preserved as an external mould in an ironstone concretion from the Sandgate Beds, found at Parham Park, Sussex (BM(NH) 9145, G. A. Mantell Collection, (see pl. 6, fig. 15).

The ornament of this medium-sized, turreted gastropod consists of three primary and three secondary spiral cords. It has a distinct linear, impressed suture and opisthocyrt growth lines between the sutures. The whorls are not flat-sided, (in fact they are concavo-convex) and the spiral cords are carinate, or rounded, not 'ribbon-like'. Axial ornament, apart from the collabral threads, is lacking. A slight distortion in the smooth opisthocyrt curve wherever the growth line crosses a spiral cord produces a wavy effect. Unfortunately, neither the abapical portion of the body whorl, nor the aperture are preserved.

VI. CONCLUSIONS

The need for exhaustive re-examination and re-evaluation of existing collections and type material has been repeatedly mentioned in the discussion above and can only be emphasized again here. Before the taxonomy of the Cerithiacea can be revised, it is necessary to improve upon the incomplete information currently available by collecting additional material. Admittedly the task of revision is complicated by the limitations of the characters that are used to distinguish fossil gastropods, while their poor preservation adds to this difficulty. Yet, the careful collecting advocated by present-day palaeontologists should enable these problems to be surmounted. The important morphological and ornamental variation of Cretaceous gastropods can be satisfactorily assessed, once accurate information on their stratigraphical occurrence is produced. These conclusions would then contribute to and facilitate our understanding of their phylogenetic and palaeoecological relationships.

The family Cerithiidae became conspicuous during the Cretaceous and during that period experimented with the form of the aperture and anterior canal. Fossil evidence is sparse and consequently, our knowledge of the forms which are thought to be transitional between either the Procerithiidae, or the more cerithiid-like Eustomidae, and true cerithiids is very limited. A similar situation occurs with their descendants. In order to achieve a re-assessment of these families, a full understanding of the derivation of the anterior canal is vital. Critical genera such as *Ageria, Cimolithium* and *Uchauxia* require further investigation, and determination of the phylogenetic position of *Metacerithium, Exechocirsus* and *Campanile* is equally important. Cox (1965 : 158) briefly mentioned the possibility that difficult groups might prove to be polyphyletic (he referred to this while discussing the origin of *Exelissa*, a genus of the Procerithiidae), but did not proceed to discuss the taxonomic implications of such a suggestion. It would provide an easy explanation of the morphological diversity apparent in '*Rhabdocolpus*' but careful consideration is necessary before such a theory can be followed.

The variation in ornament shown by several of the Cretaceous gastropods discussed here, is not thoroughly understood. In some genera, e.g. *Metacerithium*, ornament is said to be basically stable, while in others, e.g. *Bathraspira* it would appear to alter very quickly. Further, the significance of sculptural variation within a species, such as that shown by *Exechocirsus saundersi* (Woods), is also not fully appreciated. It has been suggested that the smaller Yorkshire specimens of this species might be explained as an example of ecotypic variation. The results of the detailed study recommended above should assist in providing an answer to these questions.

Among more detailed points for consideration is the verification and explanation of the occurrence of several species of the same genus at a particular horizon, e.g. three species of ?*Rhabdocolpus* in the Crackers Bed of the Lower Aptian in the Isle of Wight. There are also certain elements of doubt concerning the generic identification of several species that are considerably larger than the normal size of the genus to which they are assigned. In classifying Cretaceous gastropods 'size' is frequently used as a guide, in a subconscious and perhaps, quite illogical manner. If some disparity occurs, the correctness of the determination begins to be doubted. This is certainly true for the Upper Cretaceous specimens of *Nerineopsis* described in the paper and also for the Upper Albian species *Seila iglali*.

A better understanding of the relationship of Tertiary and Recent gastropods is to a large extent dependent upon earlier forms. The origin and early evolution of many Recent prosobranch families occurred during the Cretaceous period and the past neglect and inadequate descriptions of gastropods of this age needs to be remedied.

It is hoped that this paper will provide some of the preliminary data necessary for a more detailed and sophisticated appraisal of Cretaceous gastropods, and also that it will serve to pose a few of the questions needing investigation before such a study can be undertaken.

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PLATE 1

FIGS. 1 & 2. ***Nerineopsis melburiensis*** sp. nov.
Lower Cenomanian, Chloritic Marl, Melbury Park, nr. Shaftesbury, Dorset.
Holotype GSM 93752

Fig. 1. Apertural view. ×2·5.

Fig. 2. To show ornament of spiral cords. ×2·5.

FIGS 3 & 4. ***Nerineopsis cuckhamsliensis*** (Woods)

Fig. 3. Holotype, Sedgwick Museum B 4443, Chalk Rock, Turonian, Cuckhamsley, Wilts. ×2.

Fig. 4. BM(NH) G 48978, Chalk Rock, Holaster planus Zone, Hill End Pit, nr. Hitchin, Herts. ×3·5. Silicone rubber mould from natural external shell impression.

FIGS 5–8. ***Nerineopsis aculeatum*** (Sharman & Newton), 1896

Fig. 5. BM(NH) G 55220, To show later ornament. ×6.

Fig. 6. BM(NH) G 55191, To show general ornament. ×6.

Fig. 7. BM(NH) G 55222, Lectotype. ×6.

All from Speeton Clay, Speeton, Yorks., G.W. Lamplugh Coll'n.

Fig. 8. GSM 93749, General ornament and columella. ×4. Speeton Clay, Speeton, Yorks.

FIGS 9 & 12. ***Nerineopsis subattenuatum*** (d'Orbigny)

Fig. 9. GSM 93687. ×3.

Fig. 12. BM(NH) GG 5610, C.W. Wright Coll'n. Both from Lower Aptian, Forbesi Zone, Crackers Bed, Lower Greensand, Chale Bay, Isle of Wight.

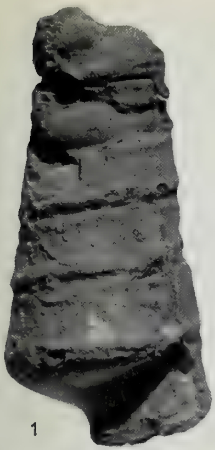
FIGS 10 & 11. ***Nerineopsis coxi*** sp. nov.
Gault, Folkestone, Kent, J.S. Gardner Coll'n.

Fig. 10. BM(NH) GG 6474. ×4.

Fig. 11. BM(NH) GG 6475, Holotype. ×4.

FIG. 13. ***Nerineopsis claxbiensis*** sp. nov.
Claxby Beds, Lower Hauterivian, Nettleton, Lincs.
BM(NH) GG 5612, Holotype. ×4.

FIG. 14. ***Nerineopsis adeli*** sp. nov.
Upper Chalk, Springbank, nr. Coagh, County Derry, Northern Ireland.
GSM 93753, Holotype. ×3.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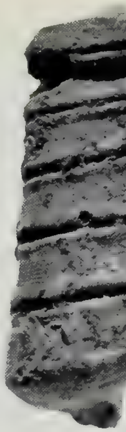
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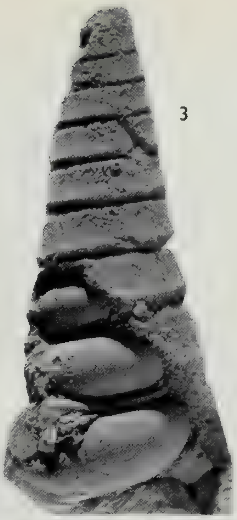
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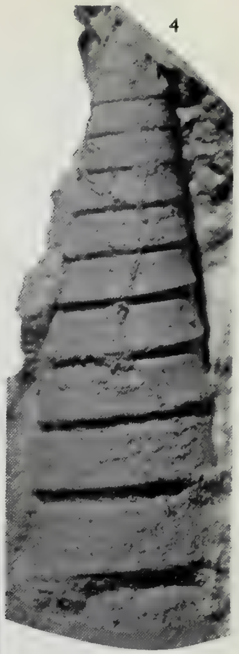
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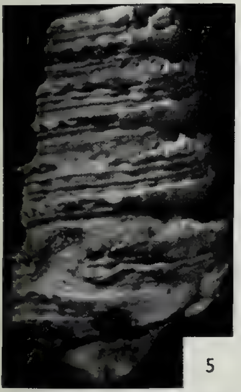
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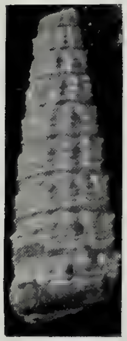
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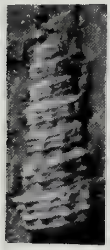
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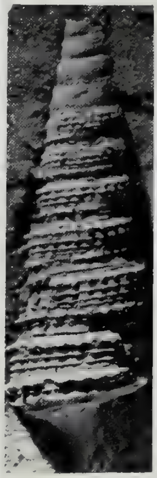
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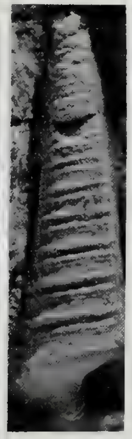
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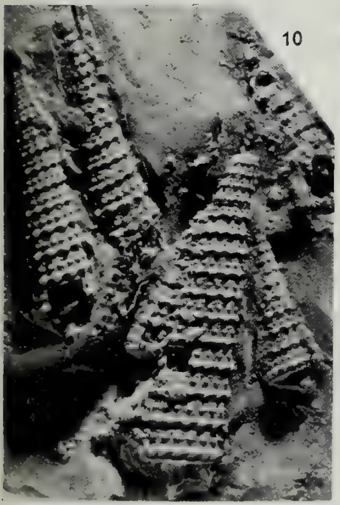
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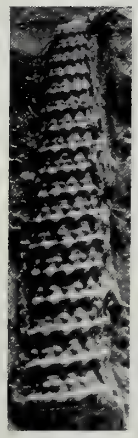
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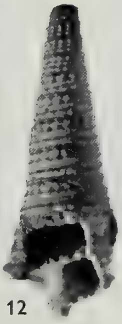
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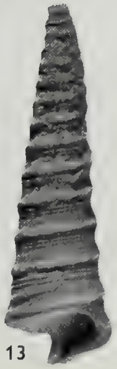
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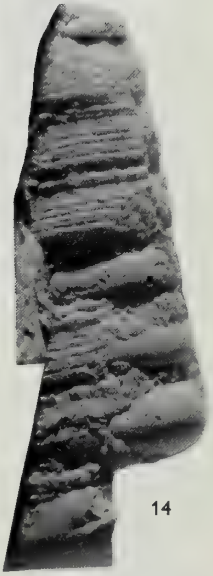
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PLATE 2

FIGS 1 & 2. ***Cirsocerithium subspinosum*** (Deshayes)
Gault, Albian, Folkestone, Kent.

Fig. 1. Sedgwick Museum B 32530. ×5.

Fig. 2. BM(NH) GG 20746, (specimen is now slightly damaged). ×6.

FIGS 3 & 4. ***Cirsocerithium nooryi*** sp. nov.
Lower Chalk, Cenomanian, Ditchling, Sussex.
BM(NH) 98208, Holotype. ×3.

FIG. 5. ***Cimolithium*** aff. ***eleanorae*** Allison.
Cenomanian, Charlton Bay, Devon.
BM(NH) G 74550. ×2.

FIG. 6. ***Cimolithium ascheri*** Wollemann.
Neocomian, Speeton Clay, Speeton, Yorks.
BM(NH) G 67942. ×2.

FIG. 7. ***Cimolithium*** cf. ***ascheri*** Wollemann.
Barremian, Cementstone Group, Cayton Bay, Yorks.
BM(NH) GG 20820. ×7.

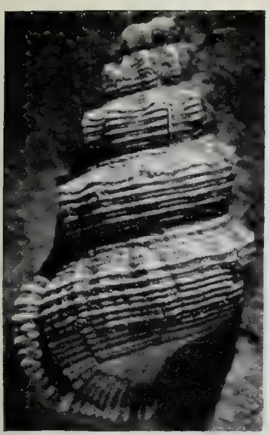
FIG. 8. ? ***Cirsocerithium kirkaldyi*** sp. nov.
Ferruginous Sands, Lower Greensand, Aptian, Shanklin, Isle of Wight.
BM(NH) GG 5603 Holotype. ×4.

FIGS 9 & 10. ***Cimolithium ascheri*** Wollemann.
Holotype 414–415, ×2, in Geologisch-Palaeontologisches Institut, Georg-August Universität, Göttingen; Neocomian, Bohnenkamp nr. Querum, Sarstedt, North Germany.

FIGS 11 & 12. ***Nudivagus morrisi*** sp. nov.
Ferruginous Sands, Upper Aptian, ? Group xiv, Lower Greensand, Shanklin, Isle of Wight.
Holotype, Geological Survey Museum 2252. ×2.

Fig. 11. Silicone rubber mould from natural impression of external ornament. Note growth lines.

Fig. 12. Latex rubber mould from same specimen, which shows spiral threads.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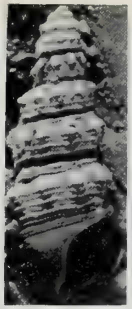
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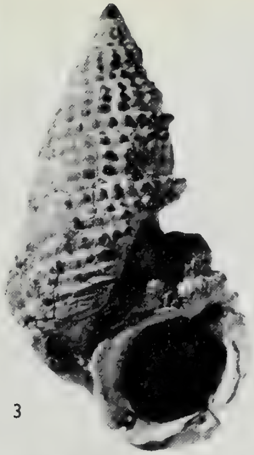
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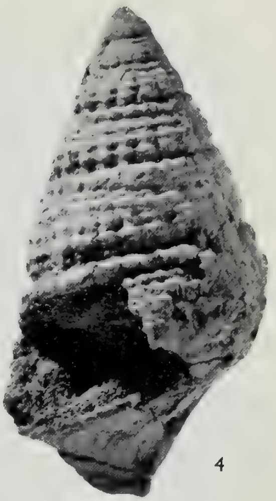
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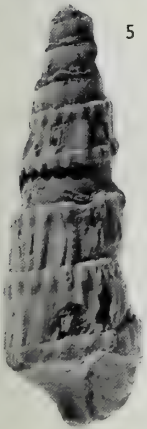
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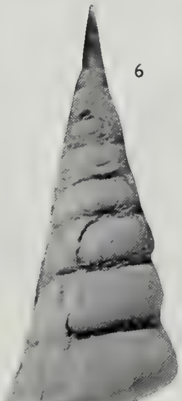
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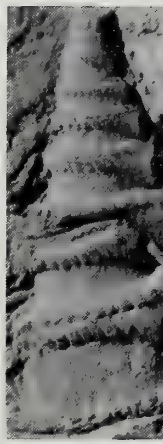
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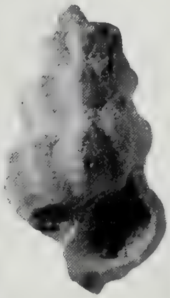
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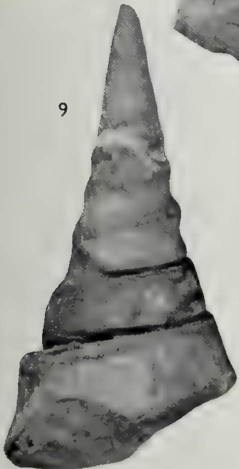
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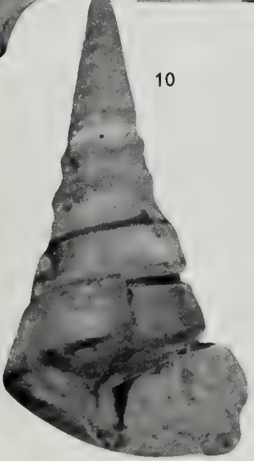
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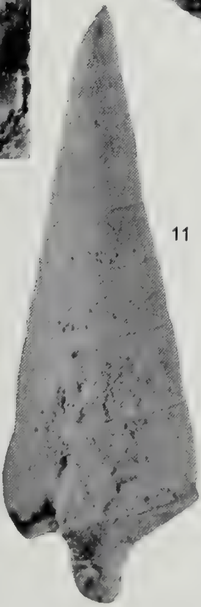
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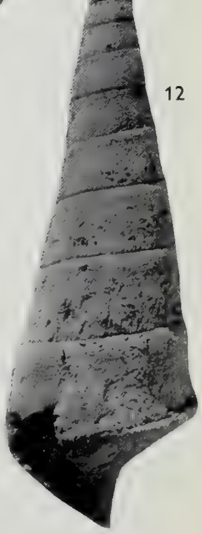
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PLATE 3

FIG. 1. ***Bathraspira tecta*** (d'Orbigny)
BM(NH) GG 6227.

Silicone rubber cast of external mould preserved in nodule from the Regularis Subzone, Tardefurcata Zone, Albian, Arnold's Pit, Billington Crossing, Leighton Buzzard, Beds. C.W. Wright Collection. ×4.

FIG. 2. ***Bathraspira*** ? ***tecta*** (d'Orb)
BM(NH) GG 20790, Gault, Albian, Folkestone, Kent. J. S. Gardner Collection. ×6.

FIG. 3. ***Bathraspira shanklinensis*** sp. nov.
BM(NH) G 20956 Lower Greensand, Ferruginous Sands, ? Perna Bed, Aptian, Redcliff, Sandown, Isle of Wight. Caleb Evans Collection. ×2.

FIGS 4–6. ***Bathraspira shanklinensis*** sp. nov.
BM(NH) GG 5602, Ferruginous Sands, Lower Greensand, Upper Aptian, Shanklin, Isle of Wight. Holotype. C. W. Wright Collection.
Fig. 4. ×4.
Fig. 5. ×3.
Fig. 6. ×3.

FIG. 7. ***Bathraspira fouadi*** sp. nov.
Paratype, Sedgwick Museum B 32524, Gault Albian, Folkestone, Kent, Wiltshire Collection. ×3.

FIG. 8. ***Bathraspira fouadi*** sp. nov.
BM(NH) G 71562 Gault, Albian, Folkestone, Kent. ×3.

FIG. 9. ***Bathraspira brightoni*** sp. nov.
BM(NH) 34843 Upper Greensand, Blackdown, Devon. ×3 approx.

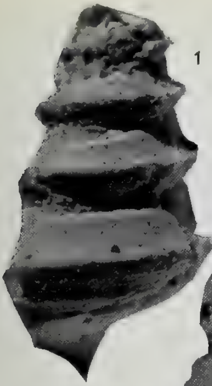
FIG. 10. ***Bathraspira cleevelyi*** sp. nov.
BM(NH) GG 5607, Holotype ? Regularis Subzone, Tardefurcata Zone, Lower Albian, Leighton Buzzard, Beds., or Bed 5, Ford Place, nr. Wrotham, Kent. C.W. Wright collection. Silicone rubber cast of external mould in nodule. ×2·5.

FIGS 11 & 15. ***Bathraspira*** cf. ***brightoni*** sp. nov.
BM(NH) GG 20791 Gault, Albian, St. Florentin, Yonne, France.
Fig. 11 shows strength of spirals and indications of growth lines. ×4.
Fig. 15 shows spiral ornament. ×4.

FIG. 12. ***Bathraspira fouadi*** sp. nov.
BM(NH) G 73795 Holotype. Gault, Albian, Folkestone, Kent. J. S. Gardner Collection. ×5.

FIG. 13. ***Bathraspira fouadi*** sp. nov. ? var.
BM(NH) G 73797 Gault, Albian, Folkestone, Kent. J. S. Gardner Collection. ×2.

FIG. 14. ***Bathraspira brightoni*** sp. nov.
BM(NH) G 73796 Holotype. Gault, Albian, Folkestone, Kent. J. S. Gardner Collection. ×3 approx.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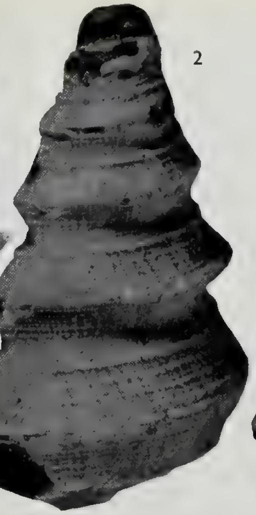
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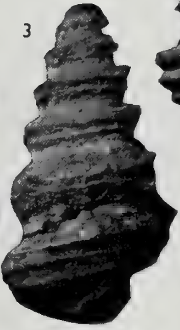
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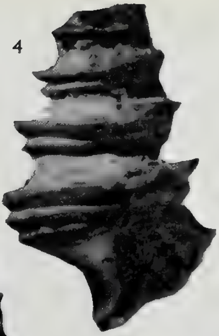
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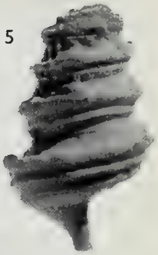
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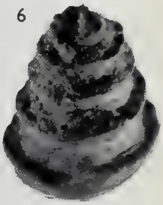
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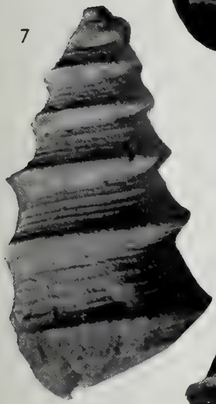
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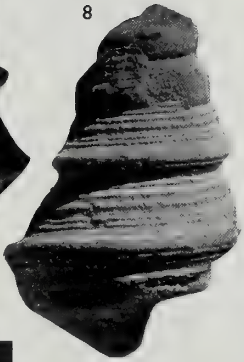
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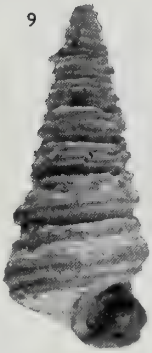
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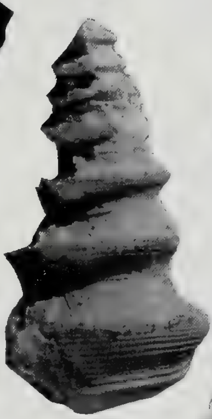
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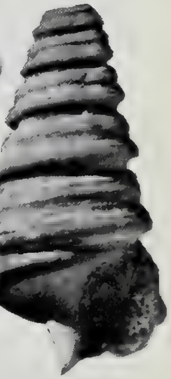
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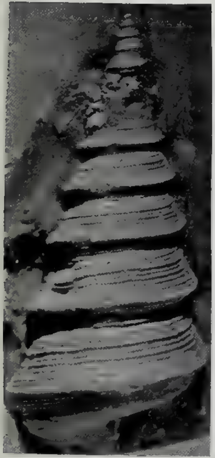
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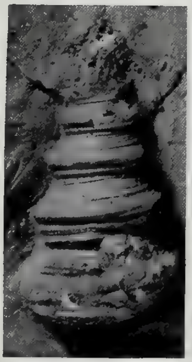
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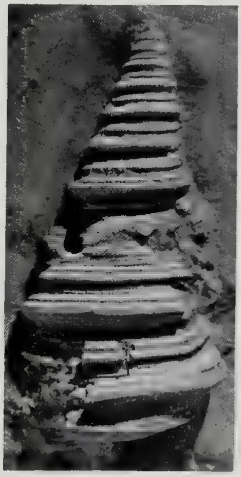
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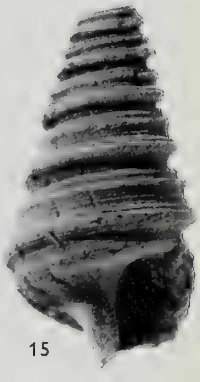
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PLATE 4

FIGS 1 & 6. ***Metacerithium*** aff. ***trimonile*** (Michelin)
Gault, Albian, Folkestone, Kent.

Fig. 1. BM(NH) G 73793. ×3·25.
Fig. 6. Geological Survey Museum. 93725. ×3.

FIGS 2, 3, 7, 8 & 10. ***Metacerithium trimonile*** (Michelin)
Gault, Albian, Folkestone, Kent. J. S. Gardner Collection, BM(NH)

Fig. 2. G 73794. ×3.
Fig. 3. GG 6472. ×3.
Fig. 7. GG 6470. ×3.
Fig. 8. GG 6471. ×3.
Fig. 10. GG 6476. ×4.

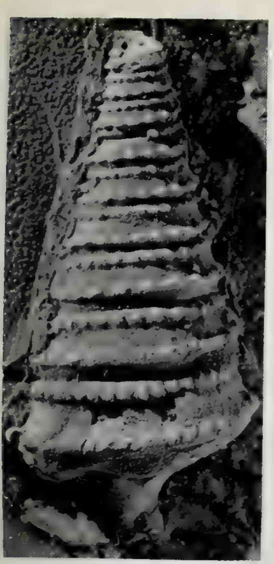
FIG. 9. ***Metacerithium*** ? sp. nov
Sedgwick Museum, B 32530, Albian, Gault, Folkestone, Kent. ×3.

FIG. 4. ***Metacerithium*** aff. ***ornatissimum*** (Deshayes)
Sedgwick Museum B 32518, Gault, Albian, Folkestone, Kent. ×3.

FIG. 5. ***Metacerithium ornatissimum*** (Deshayes)
BM(NH) GG 5601. C. W. Wright Collection, Cenomanian,
Schloenbachia varians Zone. Aston Clinton, Bucks. ×3.

FIG. 11. ***Metacerithium*** aff. ***ornatissimum*** (Desh.)
Geological Survey Museum 1698; Gault, Albian, Folkestone, Kent. ×3.

FIG. 12. ***Metacerithium ornatissimum*** (Desh.)
BM(NH) G 28908. ×3. Cenomanian varians Zone. Bed.1. Merstham, Surrey.
Collected. A. G. Davis & Ref'd. Davis (1923).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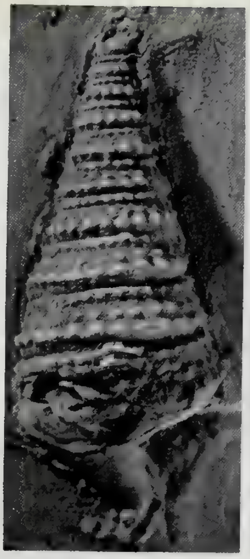
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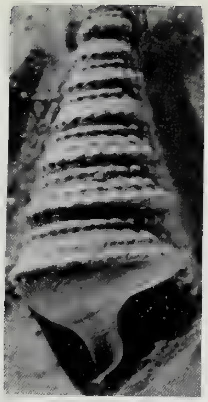
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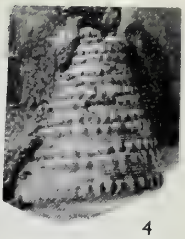
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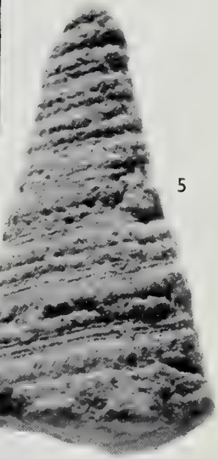
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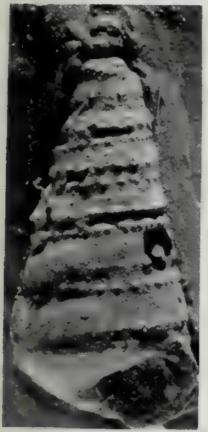
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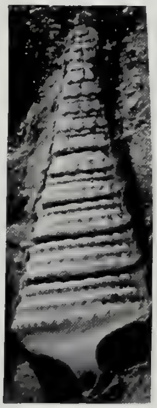
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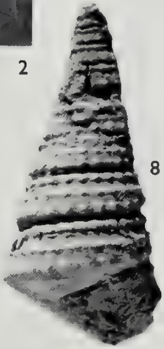
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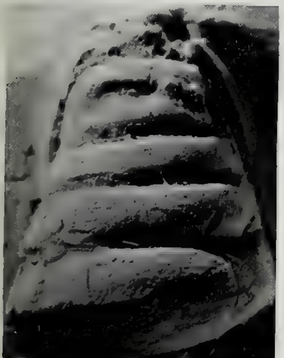
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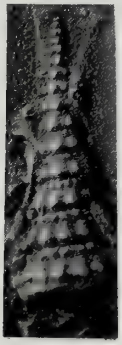
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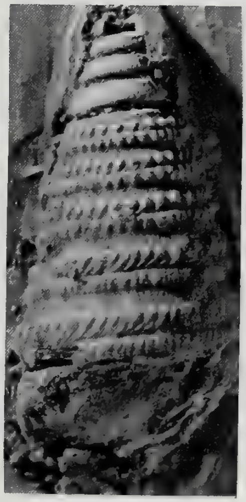
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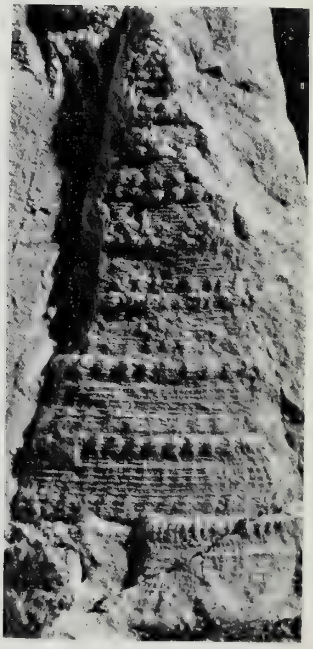
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PLATE 5

Figs 1–5 ? ***Rhabdocolpus forbesianum*** (d'Orbigny)

Lower Greensand, Crackers Bed, Lower Aptian, Forbesi Zone, Atherfield, Isle of Wight.

Figs 1–4. Stereoscan.

Fig. 1. BM(NH) GG 20850. ×20.

Fig. 2. BM(NH) GG 20848, showing the ornament of the early whorls ×23 .

Fig 3. Geological Survey Museum 2275, Lectotype from type series. ×23.

Fig. 4. BM(NH) GG 20845. ×56.

Fig. 5. BM(NH) GG 5609. ×5.

Fig. 7. ? ***Rhabdocolpus melvillei*** sp. nov.

Lower Greensand, Crackers Bed, nr. Atherfield Point, Isle of Wight.

Holotype, Sedgwick Museum B 27340, Wiltshire Collection. ×5.

Figs 6, 12 & 13. ? ***Rhabdocolpus*** ? ***clementinum*** (d'Orb)

Lower Greensand, Crackers Bed, Aptian, Atherfield, Isle of Wight. Stereoscan. ×23.

Fig. 6. BM(NH) GG 20841.

Fig. 12. BM(NH) GG 20842.

Fig. 13. BM(NH) GG 5694.

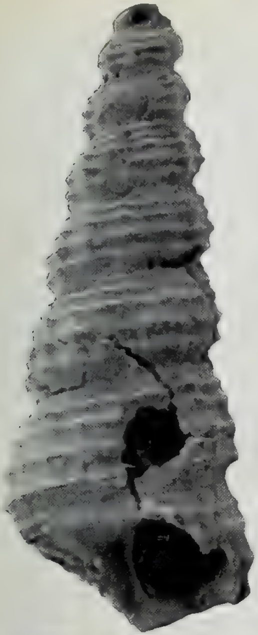
Figs 8–11. ***Metacerithium turriculatum*** (Forbes)

Lower Greensand, Crackers Bed, Atherfield, Isle of Wight.

Fig. 8. BM(NH) G 74602. ×5.

Figs 9 & 11. BM(NH) GG 20814, J. E. Lee Collection. ×5, ×7.

Fig. 10. Geological Survey Museum 2253, Specimen on left is the Holotype. ×3.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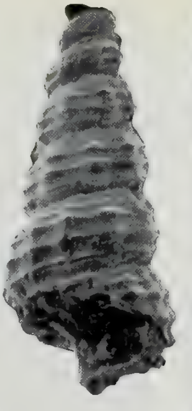
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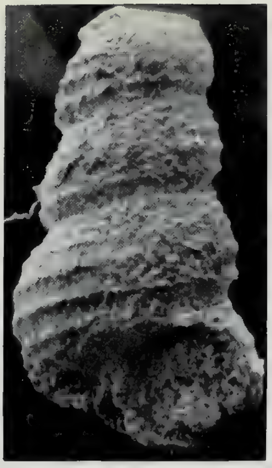
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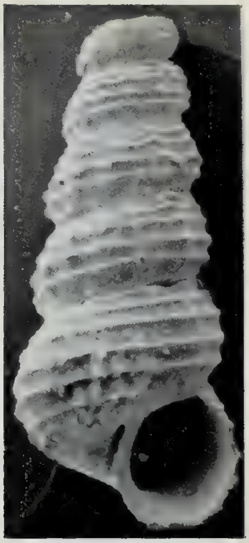
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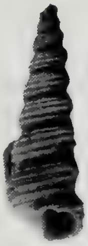
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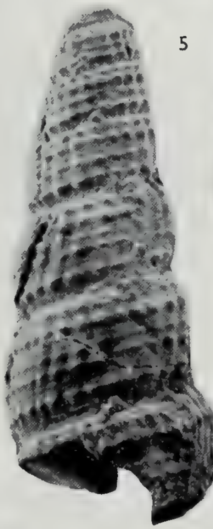
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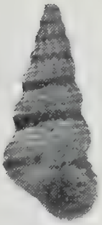
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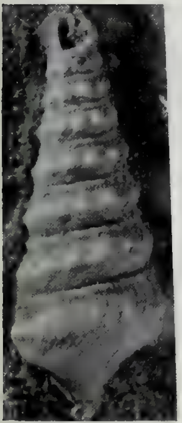
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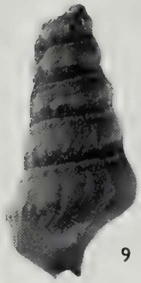
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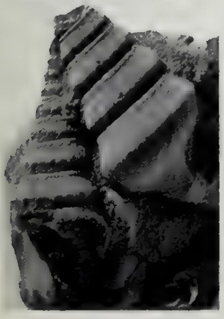
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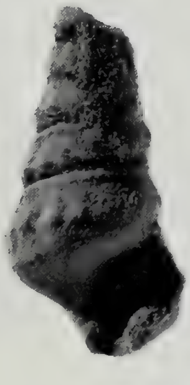
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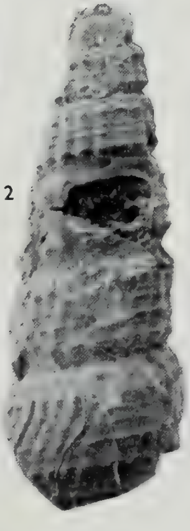
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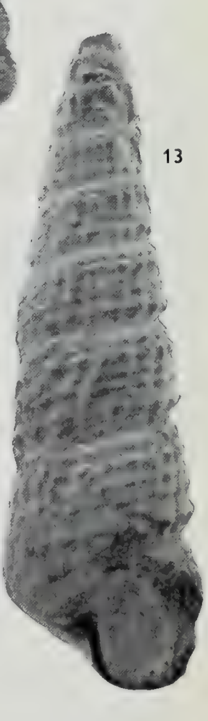
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PLATE 6

Figs 1 & 2. ? ***Campanile cenomanica*** sp. nov.
BM(NH) GG 18686. ? Cenomanian, Dorset. ×2.

Figs 3 & 4. ***Uchauxia badri*** sp. nov.
Sedgwick Museum B 44632. Upper Greensand, Albian, Blackdown, Devon. ×6.

Figs 5 & 6. ***Uchauxia wisei*** sp. nov.
C. W. Wright Collection. Claxby Ironstone, Valanginian-Hauterivian, Nettleton, Lincs.
Fig. 5. BM(NH) GG 5611. ×3·5.
Fig. 6. BM(NH) GG 6161 Holotype. ×3.

Fig. 7. ***Uchauxia*** sp.
BM(NH) G 73788. Gault, Albian, Folkestone, Kent. J. S. Gardner Collection. ×6.

Fig. 8. ***Cerithiella praelonga*** (Deshayes)
BM(NH) 72024. Middle Eocene, Bracklesham Beds, Bracklesham Bay, Hants. ×5.

Fig. 9. ***Cerithiella devonica*** sp. nov.
Sedgwick Museum B 44633. Upper Greensand, Albian, Blackdown, Devon. ×5.

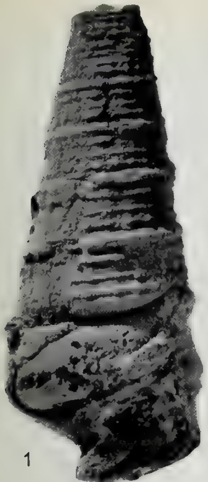
Fig. 10. ***Cerithiella atherfieldensis*** sp. nov.
Sedgwick Museum B 27334. Lower Greensand, Crackers Bed, Lower Aptian,
Forbesi Zone, Atherfield, Isle of Wight. ×3.

Fig. 11. ***Seila iglali*** sp. nov.
BM(NH) G 16084. Upper Greensand, Albian, Combe Raleigh Hill,
nr. Honiton, Devon. W. Vicary Collection. ×4.

Fig. 12. ***Orthochetus hantoniensis*** sp. nov.
BM(NH) G 70130. Aptian, Atherfield, Isle of Wight. P. Cambridge Collection. ×5.

Figs 13 & 14. ***'Orthochetus' helmyi*** sp. nov.
Gault, Albian, Folkestone, Kent. ×3.
Fig. 13. BM(NH) G 10500, Holotype.
Fig. 14. BM(NH) G 71988.

Fig. 15. ***'Orthochetus'*** sp. nov.
BM(NH) 9145, Lower Greensand, Sandgate Beds, Upper Aptian,
Parham Park, Sussex. G. A. Mantell Collection. ×3.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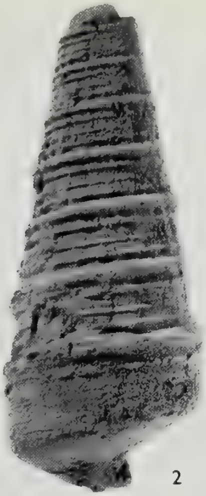
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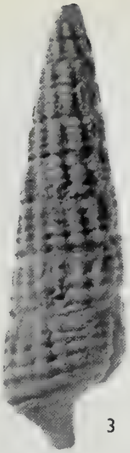
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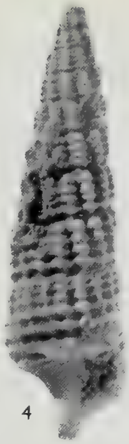
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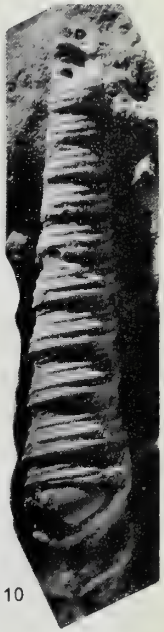
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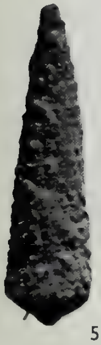
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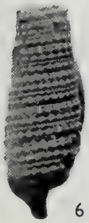
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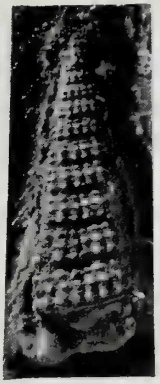
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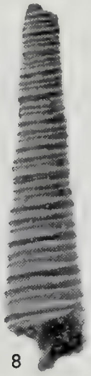
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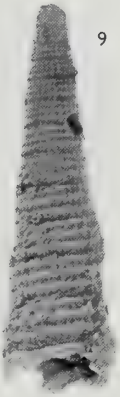
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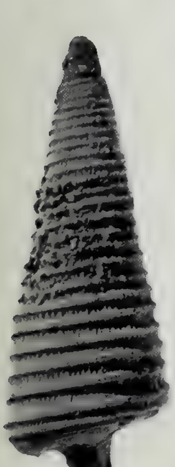
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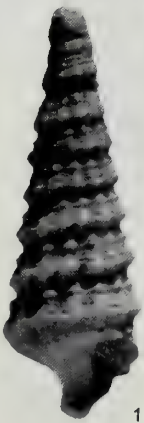
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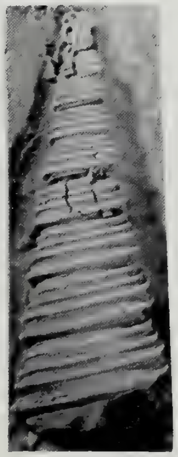
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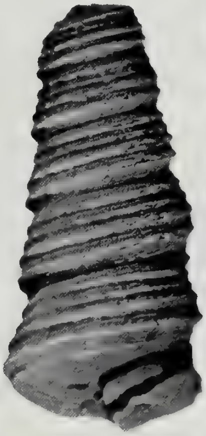
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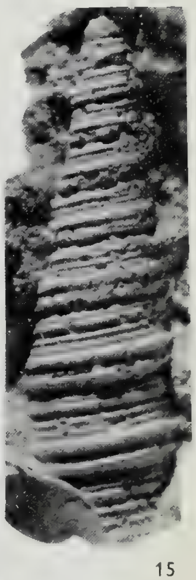
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PLATE 7

Figs 1 & 2. ***Exechocirsus*** aff. ***saundersi*** (Woods)
Cretaceous, Turonian, Chalk Rock, Holaster planus Zone;
Hitch Wood Pit, near Hitchin, Herts.

Fig. 1. BM(NH) GG 20821; shows variation in ornament i.e. weakly developed tubercles and the presence of intermediate (or secondary) spirals. Both C. W. Wright Collection, and silicone rubber moulds from external impressions. ×2.

Figs 3–5. ***Exechocirsus saundersi*** (Woods)

Fig. 3. BM(NH) GG 66724; Turonian, Chalk Rock, Blackwell Hall Farm, Latimer, Bucks. Silicone rubber mould. ×2.

Fig. 4. BM(NH) G 67704; Turonian, Chalk Rock, Dover, Kent. A. W. Rowe Collection. Silicone rubber mould. ×4.

Fig. 5. Sedgwick Museum B 4459, Holotype; Turonian, Holaster planus Zone, Cuckhamsley, North Farnborough, Berks. Silicone rubber mould. ×3.

Figs 6–7. ***Exechocirsus pustulosus*** (J. de C. Sowerby) 1833.
BM(NH) G 17916; Holotype; Upper Cretaceous, Gosau, Austria. ×1.

Figs 8 & 9. ***Exechocirsus*** aff. ***saundersi*** (Woods)
BM(NH) G 60542–60543.

Silicone rubber moulds from impressions of each half of the same shell. No other information available. ×3.

Figs 10 & 11. ***Exechocirsus*** aff. ***subpustulosus*** Pčhelincev

Fig. 10. BM(NH) G 16134.

Fig. 11. BM(NH) G 73798.

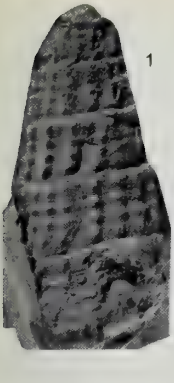
Both from the Albian, Haldon, Devon; W. Vicary Collection. ×2.

Figs 12–14. ***Exechocirsus*** aff. ***saundersi*** (Woods)

Fig. 12. BM(NH) GG 20823, Hitch Wood Pit, nr. Hitchin, Herts. C. W. Wright Collection. Silicone rubber mould. ×2.

Fig. 13. BM(NH) GG 5934. Turonian, Holaster planus Zone, Kiplingcotes, E. Yorks. C. W. Wright Collection. Silicone rubber mould. ×2.

Fig. 14. BM(NH) GG 5983. Same locality as above; natural mould. ×4.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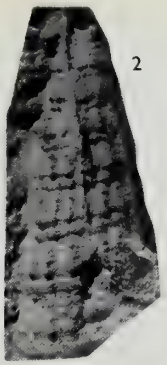
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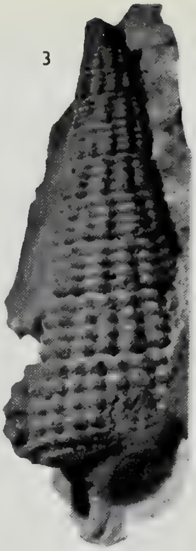
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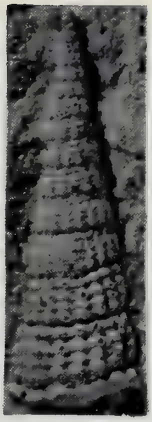
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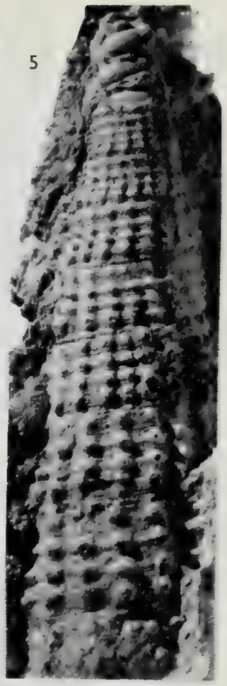
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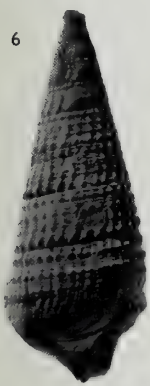
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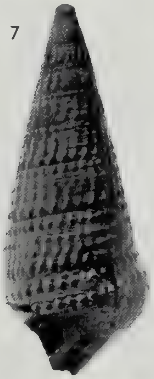
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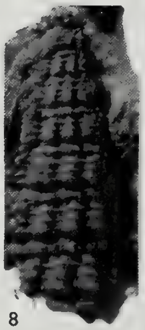
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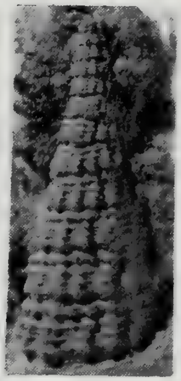
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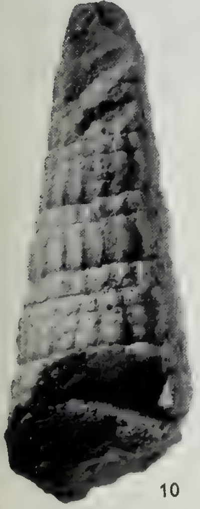
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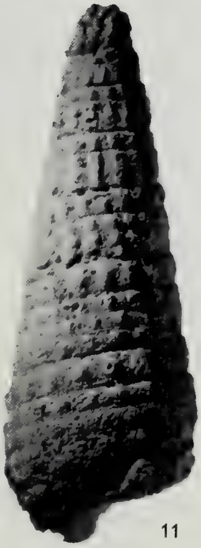
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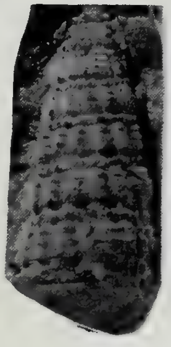
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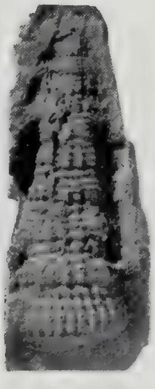
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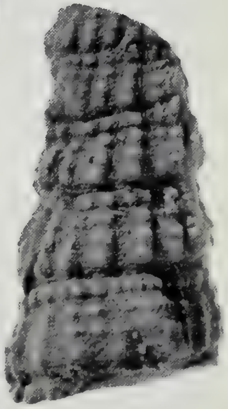
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PLATE 8

FIGS 1–4 & 6. ***Ageria gaultina*** sp. nov.

Albian, Gault, Folkestone, Kent. J. S. Gardner Collection. BM(NH) specimens

Fig. 1. GG 6473. Holotype. ×4.

Fig. 2. GG 20741. ×3.

Fig. 3. GG 20742. ×3. ? Bed v, Lower Gault (fide Dr. H. G. Owen), shows slight variation in ornament.

Fig. 4. GG 20862. Shows the ornament of the earlier whorls. ×4.

Fig. 6. GG 20857. ×3.

FIG. 5. ***Ageria gaultina*** sp. nov.

Albian, Osmington, Dorset, BM (NH) G49804. ×3·5.

FIGS 7–10. ***Ageria costata*** (J. de C. Sowerby)

Upper Greensand, Albian; Blackdown, Devon. BM(NH) specimens

Fig. 7. 71382. Shows aperture. ×4.

Fig. 8. 43674. Holotype, Sowerby Collection. ×5.

Fig. 9. 34844. Also shows aperture. ×6.

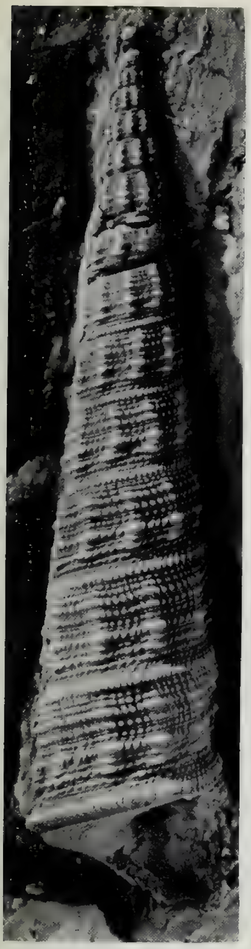
Fig. 10. GG 20832. ×3.

FIGS 12. ***Ageria costata*** (J. de C. Sowerby)

BM(NH) G 71095, Albian Upper Greensand; Bed 12, Peak Hill,
nr. Sidmouth, Devon. H. F. Metcalfe Collection. ×3.

FIG. 13. ? ***Ageria angustata*** (d'Orbigny)

BM(NH) GG 20740. Neocomian, Claxby Beds, Nettleton, nr. Caiston, Lincs
C. W. Wright Collection. ×5.



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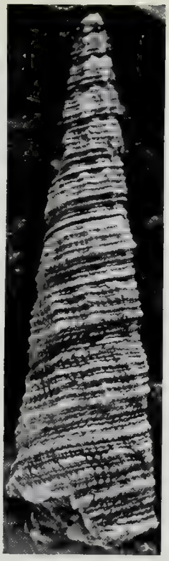

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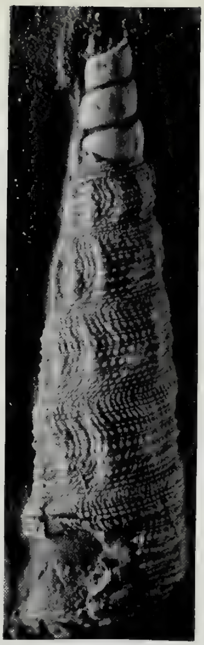

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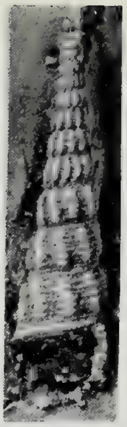

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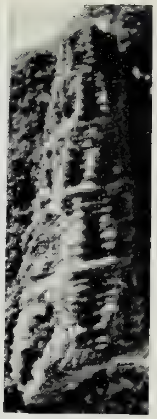

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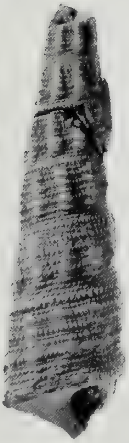

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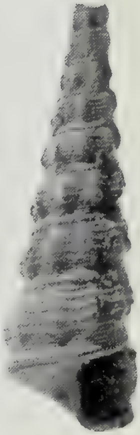

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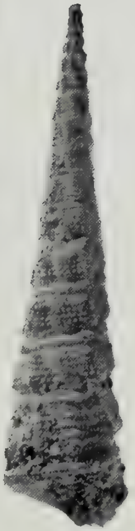

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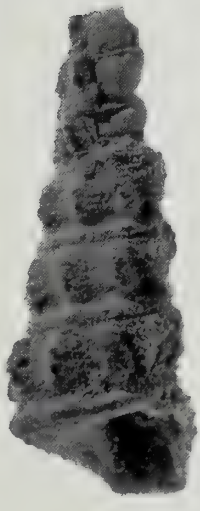

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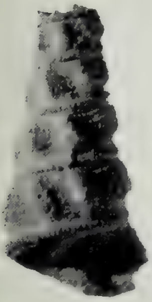

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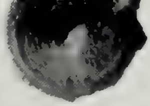

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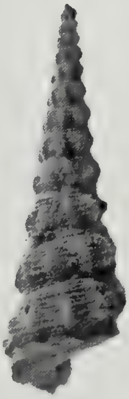

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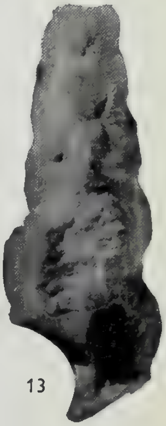

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A REVIEW OF SOME ENGLISH PALAEOGENE NASSARIIDAE, FORMERLY REFERRED TO *COMINELLA*

BRITISH MUSEUM
4 JUL 1973
NATURAL HISTORY

C. P. NUTTALL

AND

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Pp. 177–219; 9 *Plates*; 1 *Text-figure*

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SYNOPSIS

English Palaeogene prosobranch gastropod species, previously assigned to the Tertiary and living New Zealand genus *Cominella* (Buccinidae or Cominellidae of Buccinacea), are reviewed. New genera are described to accommodate these English species and their European relatives. They are assigned to the Nassariidae (Buccinacea) on the characters of their fascioles and columellae, in particular the presence of a terminal columellar plait. Like living Nassariidae, they probably lived in warm seas, in shallow water, possibly intertidally. Their known distribution, both in Europe and beyond, is summarized. *Colwellia* nov. gen. occurs both in the European and the United States west coast Eocene (California to Washington State) where it is represented by species usually assigned to *Molopophorus*. Most other species assigned to the latter genus also appear to belong to the Nassariidae. Its type species, *M. striatus* (Gabb) seems not to belong to the family but to be a synonym of *Brachysphingus* which is shown to lack the characteristic terminal columellar plait. Palaeocene *Thanetinassa* nov. gen. shows certain similarities to the later Palaeogene *Phos*-like (Buccinidae) genera *Tritiaria*, *Buccitriton* and to *Sagenella* (Nassariidae), all from the U.S. south-eastern province. This publication is a preliminary to a more intensive review of the Nassariidae and their possible relationship with the *Phos*-like group.

The following new genera of Nassariidae are described:—*Pseudocominella*, *Desorinassa*, *Whitecliffia*, *Colwellia*, *Keepingia* and *Thanetinassa*. The following new species are described from the Hampshire Basin. Eocene (Ypresian):—*Desorinassa williamsi*; Late Priabonian:—*Pseudocominella semicostata*, and *Whitecliffia tumida*. Several Palaeogene species, including *Buccinum canaliculatum* J. de C. Sowerby and *B. montense* Briart & Cornet are shown to be unrelated to the Nassariidae.

INTRODUCTION

THE present study started as a result of a request for identification of a specimen from the English Lower Eocene which proved to belong to an undescribed species. It is one of a small group of species in need of revision which are normally assigned to the living New Zealand genus *Cominella*.

The genus *Cominella* was erected by Gray (1850 : 72) who assigned to it nine living species from New Zealand, Australia and South Africa. Iredale (1918 : 34) designated as type species the first mentioned, *Buccinum testudineum* Lamarck from New Zealand. He also selected the living South African species *Buccinum cinctum* Röding (= *porcatum* Gmelin, preoccupied) as type species of his new genus *Burnupena*.

During the latter part of the nineteenth century the name *Cominella* came to be almost universally applied to a group of European species, most of which are now assigned to the new genera described here. The designation by Cossman (1901 : 149) of *Buccinum porcatum* Gmelin as type species of *Cominella* is invalid as it was not among those listed by Gray. Cossmann, unfortunately, also based his definition of the genus partly on two European Palaeogene species which he regarded as 'plesiotypes', *Buccinum gossardi* Nyst and *Buccinum desertum* Solander. He regarded *Molopophorus* from the Eocene of California as a probable synonym of *Cominella*, and (1901 : 201) stated that *Molopophorus* should be eliminated from the Nassidae (now known as Nassariidae), though expressing doubts as to the accuracy of Gabb's figure of the lectotype of *M. striatus* Gabb, the type species of *Molopophorus*. Later Cossmann indicated that he had no remaining doubts as to this synonymy after examining the type figures of another species, *Molopophorus gabbi* Dall (1909 : 45, pl. 3, fig. 8), from the Oligocene of Oregon (see Weaver, 1942 : 466). Subsequent American workers (Stewart, 1926 : 389; Vokes, 1939 : 140–141) have suggested a connection between *Molopophorus* and European Palaeogene species assigned to *Cominella*. In the present study four United States West Coast species, previously assigned to *Molpophorus*, are recognized as belonging to *Colwellia*. A re-examination of the lectotype of *Molopophorus striatus* suggests that it is a juvenile *Brachysphingus*, and that neither belong to the Nassariidae (see p. 209). All other species normally regarded as belonging to *Molopophorus* appear to have little in common either with its type species or with *Brachysphingus* and seem to belong to more than one undescribed genus. Gabb (1869 : 156, 157, pl. 26, fig. 36) in describing *Molopophorus* as a subgenus of *Bullia*, compared it with *Bullia* (*Buccinanops*) *monilifera* (Kiener) now living on the Atlantic Coast of South America. Not only the type species of *Molopophorus*, but also species assigned to that genus later, and *Brachysphingus* have been generally accepted by American authorities as members of the Nassariidae.

Some of the gross shell characters of these American Tertiary forms and the European Tertiary genera described in this paper closely resemble those found in modern Nassariidae and in *Cominella* which have fasciole regions of a broadly similar type (see Text-fig. 1). The growth lines on the neck region are bent aborally to form a ridge confluent with the adapical margin of the track of the anterior notch. The deepest point of the asymmetrically U-shaped notch is usually fairly close to the ridge. Below the ridge there is some variation. The growth lines range from regular to imbricate and are reverse S-shaped, but the upper and lower halves of the S may be of varying proportions and curvature. In true *Cominella* the notch corresponds with a raised ridge, as opposed to a groove observed in many definite Nassariidae and the fossil genera under consideration. A more important feature that the latter share with definite Nassariidae is that the columella is bent strongly to the left and bears a terminal plait. *Cominella* lacks this plait and its columella is not so strongly bent.

On these grounds these fossil genera may be assigned with confidence to the Nassariidae rather than to the Buccinidae (as constituted by Wenz, 1941 : 1151–1200; 1943 : 1201–1210), which includes the Cominellidae of Powell (1929 : 57).

Homoeomorphic, superficial, similarities between these genera and *Cominella* include the frequent development of a subsutural platform and concave ramp and the rather flexuous but basically orthocline growth lines.

Buccinum canaliculatum (J. de C. Sowerby, 1823 : 14, pl. 415, fig. 2) from the Barton Beds of the English Upper Eocene was placed in *Cominella* by Newton (1891 : 168). Cossmann (1901 : 121–123, pl. 8, figs 13, 14) selected it as the type species of his monotypic genus *Bartonia*. He compared it with '*Cominella*' *deserta* from the same formation, pointing out the differences in the features of their apertures and canals. *Bartonia canaliculata* lacks a columellar plait, its columella curves to the left and is not truncated, no ridge is formed at the adapical margin of its fasciole and the growth lines in the fasciole region are less strongly curved than in *Pseudocominella* (Text-fig. 1). It is hoped that *Bartonia*, which remains assigned to the Buccinidae (*sensu* Wenz, 1941–1943) will be treated in a future paper.

In this paper, five genera, *Pseudocominella*, *Desorinassa*, *Colwellia*, *Whitecliffia* and *Thanetinassa* are described to accommodate British and European Tertiary species previously assigned to *Cominella*. The opportunity is also taken to describe a sixth genus of the group, *Keepingia*, though it does not occur in England. The

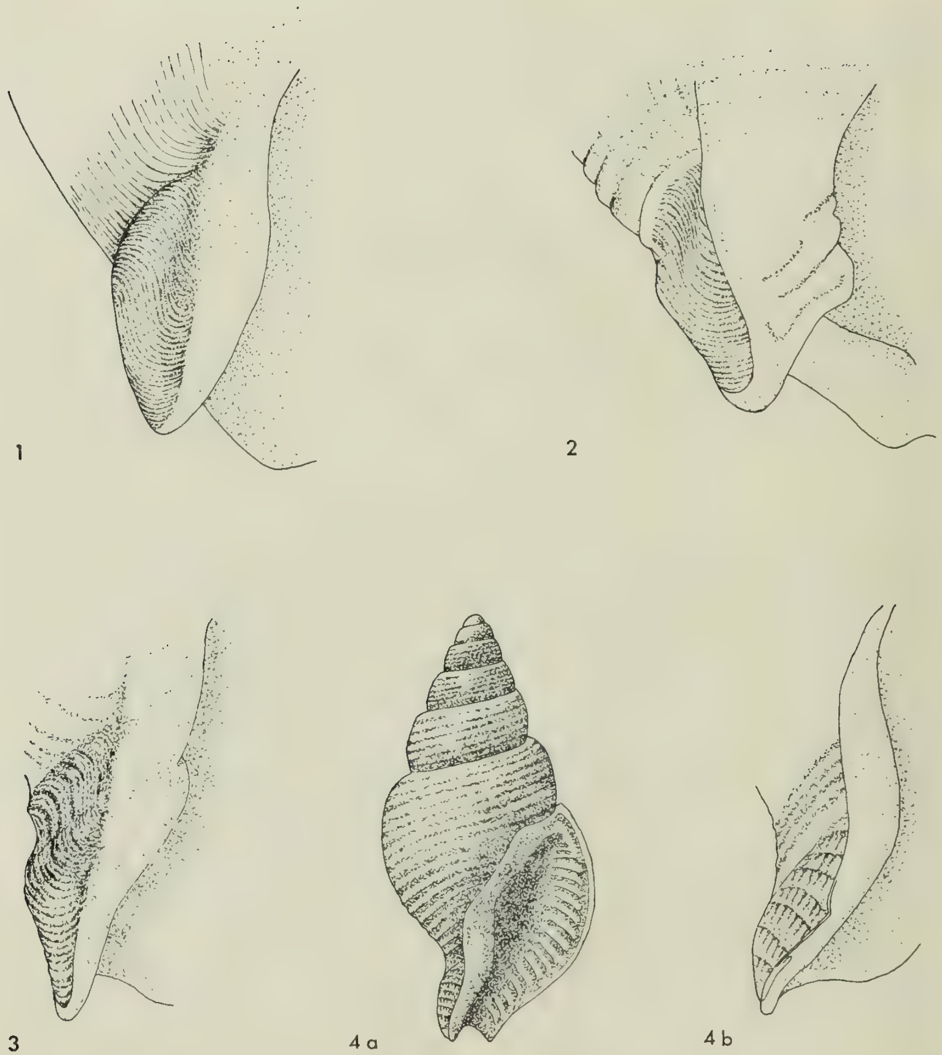

Fig. 1. Fasciole and columellar details of 1, *Cominella testudinea* (Lamarck), type species of *Cominella* (fam. Buccinidae) Recent, New Zealand, BMZD 1844.7.29.36, showing ridge above fasciole and no columellar plait (also see pl. 9, figs 11a, b), ×5. 2, *Sphaeronassa mutabilis* (Linné), type species of *Sphaeronassa* (fam. Nassariidae), Recent, Bay of Naples, BMZD 19722, showing strong ridge above fasciole, strong terminal columellar plait with weaker plaits above, ×5. 3, *Pseudocominella deserta* (Solander) type species of *Pseudocominella*, Upper Eocene, Lower Barton Beds Bed B, Barton, GG 19675 (*Ru*), showing strong ridge above fasciole, imbricate growth lines of fasciole, strong terminal columellar plait with weaker plaits above (see also pl. 1 figs 7a, b), ×5. 4a, b, *Bartonia canaliculata* (J. de C. Sowerby), type species of *Bartonia* (fam. Buccinidae), Upper Eocene Lower Barton Beds, Barton. 4a, GG 6897/1 (*Wr*), apertural view, ×2·5; 4b, GG 6897/2 detail, showing no sharp break between neck and fasciole and no columellar plait, ×7·5.

gross shell characters of these new genera are fairly similar, the main differences being in the form of the apical whorls, strength of sculpture and the strength and character of the ridging in the fasciole region.

The known distribution of these genera, in Europe and beyond, is summarized on Table 1. We have examined numerous references to *Cominella*, *'Nassa'*, *Molopophorus* and *Brachysphingus* but have found few plausible extra-European occurrences of the genera newly described here.

The recognition of these additional Palaeogene members of the Nassariidae affects our understanding of the evolution of the family. It is intended to pursue this topic in a future paper.

Although it is hoped that the specific and generic diagnoses will be sufficient to distinguish different taxa, the descriptions given here are detailed. In addition, the variation in a species from locality to locality has been illustrated and commented on as fully as possible. This policy is justified because apparently good illustrations and descriptions have proved inadequate and misleading, so that important points have only been resolved by the study of actual specimens. To quote only a few examples, it seems incredible that the European Tertiary species discussed herein should have been accepted for about one hundred years as members of the Recent New Zealand genus *Cominella* which belongs to another family, that *Buccinum montense* Briart & Cornet was not recognized as being congeneric with many Eocene species assigned to *Pollia* of the Buccinidae, that *Bartonia canaliculata* (J. de C. Sowerby) should have been considered congeneric with *Buccinum desertum* Solander, and that the French Lutetian and Auversian *Buccinum fusiforme* Deshayes should have been considered synonymous with the Bartonian *B. desertum* Solander rather than with the Auversian *Strepsidura armata* J. de C. Sowerby.

MATERIAL STUDIED

This study of English specimens is based primarily on the collections in the British Museum (Natural History). Material in the Sedgwick Museum, Cambridge, the Geological Survey Museum, London, the Sandown Museum, Isle of Wight, Institut Royal des Sciences Naturelles de Belgique, Bruxelles, Institut de Paléontologie, Muséum National d'Histoire Naturelle, Paris, and École des Mines, Paris has also been examined. In addition, much valuable information has been obtained from the stratigraphically detailed labels of several private collectors. To indicate the authenticity of various records, the collector is named when known.

The most important single collection is that of F. E. Edwards in the British Museum (Natural History). Much of his collection was obtained from workers such as Henry Keeping, who also collected the fossils from Huntingbridge listed by Fisher (1862 : 79), and it was enriched by exchange with foreign palaeontologists. It forms the basis of many published faunal lists (von Koenen, 1864; Judd, 1880; Keeping & Tawney, 1881). The British material in the Edwards collection was catalogued by Newton (1891), who included many of Edwards' manuscript names. Both the Edwards collection and Newton's catalogue may be presumed to be the

TABLE I

Distribution of some early Nassariidae

	STAGE	ENGLAND	FRANCE	BELGIUM HOLLAND	GERMANY	NORTH AMERICA (WEST COAST)	OTHER OCCURRENCES	
MIOCENE	Tortonian	—	—	—	—	—	—	
	Burdigalian	—	*K. tarbellica*	—	—	—	—	
	Aquitanian	—	***K. praecedens* ***K. aturensis*	—	—	—	—	
OLIGOCENE	Chattian	—	—	*K. bolli*	*K. bolli* *K. cassidaria* ***K. uniseriale*	—	—	
	Rupelian	—	*K. gossardi*	*K. gossardi* *W. suturosa*	*K. cassidaria* *W. suturosa*	—	**?*K. annandalei* (Nari stage)	(W. PAKISTAN)
	Lattorfian	—	—	*P. bullata* *K. gossardi* *W. suturosa*	*P. bullata* *P. bullata aspera* *W. suturosa*	—	—	
EOCENE	(Late Priabonian)	*P. deserta* *P. semicostata* *C. flexuosa* *W. suturosa* *W. tumida*	—	—	—	—	—	
	Bartonian (early Priabonian,)	*P. deserta* *P. solanderi*	—	—	*P. deserta*	*C. bretzi* *C. tejonensis*	—	
	Auversian	*P. armata*	*C. auversiense* *P. armata*	—	—			
	Lutetian	—	*P. armata*	—	—	*C. antiquata* *C. cretacea*		
PALAEOCENE	Cuisian	—	*D. acies* *D. ovata*	—	—			
	Ypresian	*D. williamsi*	—	—	—		**?*D. bonnecarrei*	(TOGO)
	Sparnacian	—	—	—	—	—		
	Thanetian	*T. bicorona* *D. desori*	*T. bicorona* *D. desori* *D. lata*	—	—	—	**?*D. suprocostata*	(AUSTRIA)

(note: specimens of species marked ** have not been examined.)

EXPLANATION TO TABLE 1

The table is compiled from:

(a) England (this paper).
(b) France: Cossmann, 1901; Deshayes, 1865; Glibert, 1960, 1963; Peyrot, 1927.
(c) Belgium & Holland: Albrecht & van der Valk, 1943; Glibert, 1954, 1957.
(d) Germany: Beyrich, 1854; Glibert, 1960, 1963; Sandberger, 1863; von Koenen, 1889.
(e) North America: Vokes, 1939; Weaver, 1942.
(f) Austria: Traub, 1938.
(g) Togo: Furon & Kouriatchy, 1948.
(h) West Pakistan: Vredenburg, 1925.

Notes. An examination of the holotype and paratype (Bayerisches Geol. Landesamt no. 3080, 3081) of *Northia* (*Cominella*) *angusta* Hölzl (1958 : 244, pl. 20, figs 16–16a) suggests that the species should be referred to *Dorsanum*. *Buccinum montense* Briart & Cornet (1871 : 30–31), referred by subsequent authors to *Cominella* is a *Pollia* (Buccinidae). Many North American species ranging from Paleocene to Miocene in age are omitted from this table. They belong to undescribed genera (see p. 209) close to those described herein. An examination of the holotype of *Cominella dertonensis* Bellardi (1882: 3, pl. 1 figs 1a, 1b) from the Middle Miocene (Tortonian) of St Agata-fossili, Italy (Instituto di Geologia, Turin, no. 11436) shows that it is not a member of the Nassariidae and is in no way related to *Pseodocominella*.

Abbreviations of generic names

C., Colwellia; D., Desorinassa; K., Keepingia; P., Pseudocominella; T., Thanetinassa; W., Whitecliffia.

main sources of the records of species in Britain quoted by Continental authorities such as von Koenen and Cossmann. Keeping's own collection in the Sedgwick Museum, Cambridge, is of particular value because of the reliability of his labels.

The publication (1933) of the late E. St. J. Burton's letter classification of horizons in the Barton Beds at the type locality Barton-on-Sea has enabled later collectors to indicate horizons more precisely than hitherto. The faunal list published by Burton was by no means complete. His own collection, now in the British Museum (Natural History), is not as valuable as it might have been since he often arranged specimens of a particular species from several horizons in the same box.

In the systematic descriptions, the localities and horizons of material which we have examined are given after the synonymy, under the heading 'Material Studied'. It has not been considered necessary to list here material in other Museums which merely complements the British Museum collections unless the record is of particular interest.

Under the subsequent heading 'Further Occurrences', we give records in the literature of those other localities and horizons from which we have not studied material. To avoid undue repetition, we have omitted those records that were probably based on the specimens which we have studied.

Explanation of abbreviations referring to sources of specimens

ANSP, Academy of Natural Sciences of Philadelphia; *CAS*, California Academy of Science; *Cu*, D. Curry Colln.; *Ed*, F. E. Edwards Colln.; *EMP*, École des Mines, Paris—invertebrate collections now being transferred to Laboratoire de Paléontologie, Institut de Géologie, Université de Paris, Orsay-91, France, under direction of M. J. Manivit; *Ho*, M. J. Hoare Colln.; G or GG (followed by number), Department of Palaeontology, British Museum (Natural History); *IRScNB*, Institut Royal des Sciences Naturelles de Belgique, Bruxelles; *Je*, P. Jennings Colln.; *K*, H. Keeping Colln.; *K&T*, H. Keeping & E. B. Tawney Colln.; *Le*, D. N. Lewis Colln.; *MNP*, Institut de Paléontologie, Muséum National d'Histoire Naturelle, Paris; *Nu*, C. P. Nuttall Colln.; *Ru*, A. J. Rundle Colln.; *St. J. B*, E. St. J. Burton Colln.; *Sedg. Mus.*, Sedgwick Museum, Cambridge; *Sand Mus.*, Sandown Museum & Public Library, Sandown, I.O.W.; *S*, F. C. Stinton Colln.; *U.Cal.*, Museum of Paleontology, University of California, Berkeley; *Wr*, A. Wrigley Colln.; *ZD*, Recent Mollusca Section, Department of Zoology, British Museum (Natural History).

LOCALITIES AND HORIZONS

Many of the British localities are still in existence, are well-known and need no further introduction. Some others, notably the New Forest (Hampshire) localities of the Bracklesham and Middle Headon Beds are either poorly known or are no longer accessible. Curry (1958) gives details and map references to most.

The following points should be noted about locality names attached to the Edwards Collection:

1. Bramshaw, Upper Bracklesham Beds, is described (Curry, 1958 : 70) under Shepherd's Gutter Bed.

2. Roydon, Middle Headon Beds, refers to Royden Manor brick pit (now overgrown) at Nat. Grid SU 320005. Curry (1958 : 29) discusses this locality under the heading 'Brockenhurst Beds'. The section was described by Keeping & Tawney (1881 : 113 and 114 footnote), the latter refers to the fact that Keeping collected the material in the Edwards Collection.

3. Brockenhurst, Middle Headon Beds. Specimens in the Edwards Collection are labelled either Brockenhurst or Whitley Ridge. Keeping & Tawney (1881 : 109) write 'The greater part of the fossils from Brockenhurst were collected by the hands of one of the authors (i.e. Keeping) and . . . dispersed into the various public and private collections. They were obtained from the (railway) cutting at Whitley . . . about (1858, when an extra track was being laid). In a footnote (pp. 109–110), they point out that they both visited the cutting in the summer of 1880, and that the rich (fossiliferous) zone would never be seen here again but that fossils could still be obtained from the spoil heaps (left from the cutting for the original single-track railway in about 1838). As it is clear from a further footnote (p. 114) that Keeping collected the Royden and Lyndhurst fossils in the Edwards Collection, it is more than likely that the same applied for Whitley Ridge. A possible explanation for some of Edwards' material being labelled 'Brockenhurst' is that it was obtained from the spoil-heaps. It seems extremely unlikely that the material came from the Victoria Tile Works at SU 316034. This locality was not mentioned by Keeping & Tawney (1881). It was in existence by 1890 and was normally worked to only a shallow depth as the weathered material near the surface produced the best-coloured products, so that the Brockenhurst shell bed was seldom exposed (Davis, 1952 : 215–216). The foregoing, however, suggests that Davis might have been mistaken in stating that Edwards had worked the local exposures. Whitley Ridge Cutting is the type locality of the Brockenhurst Beds (Curry, 1958 : 29).

4. Lyndhurst, Middle Headon Beds. Edwards' specimens were probably collected by Keeping in 1858 from pits dug on Lyndhurst Hill, to the west of Lyndhurst, the Brockenhurst Bed outcropping at about the 200 ft contour (Tawney, 1883).

The Brander Collection locality 'Hordwell' (= Hordle) quoted by Solander (1766) was the nearest village to the Barton coastal section before Barton itself was built and named.

The Middle Headon Beds have been regarded by most British workers as being of Lower Oligocene (Lattorfian) age. Recent nannoplankton zonation work by Martini & Ritzkowski (1968 : 244–247), Martini (1969 : 117–159), and Martini & Moorkens (1969 : 125–127) show that the Headon Beds are late Priabonian and that some German localities, previously regarded as Oligocene are distinctly pre-Lattorfian. Westeregeln, in part, is now regarded as being approximately equivalent to the Upper Barton Beds.

The ages accorded here to French Paris Basin localities are based on the lists given by Glibert (1960 : 3–5), and by reference to Fritel (1910).

MODE OF LIFE

Pseudocominella and its relatives appear to have lived in shallow water. *Thanetinassa bicorona*, according to Briart & Cornet (1871 : 31), is very common at some French localities, notably Châlons-sur-Vesle in the Sables Inférieurs—a shallow-water sandy deposit. The species also occurs in the coarsely-grained Thanet Sands in England. No species of the group are known from the London Clay. The only British species occurring in rocks of equivalent age is *Desorinassa williamsi* from the shallow-water Bognor Rock. *Pseudocominella armata* is rare and occurs in the rich fauna of the Upper and more clayey part of the Bracklesham Beds. No species is known from the more sandy Lower Bracklesham Beds. In the Barton Beds, species of *Pseudocominella* are known from Horizons A2 to H. *P. deserta* is never common. From the appearance of the specimens it would seem that most were obtained from the extremely fossiliferous Horizon E. *P. solanderi*, however, is extremely common in the lenticular, sandy, shell drifts of Horizon A3. Members of the group also occur in the Brockenhurst and *Venus* Beds of the Headon Series. These two latter beds represent periods of shallow marine deposition in a largely fresh and brackish water succession.

Turning again to the European Continent, many of the occurrences are consistent with a shallow-water mode of life. Examples include *P. armata* in the Calcaire Grossier and *Keepingia gossardi* in the Sables Supérieurs of the Paris Basin, *K. gossardi* and *Whitecliffia tumida* in the Belgian Oligocene and *K. cassidaria* in the late Oligocene deposits of the Mainz Basin. Finally, we note the occurrence of species of *Keepingia* in the Lower Miocene of the Bordeaux region in conjunction with *Nassarius*, *Dorsanum* and *Cyllene*, all living genera of the Nassariidae.

Nearly all the present day Nassariidae live in very shallow water and many intertidal species of the three most important genera, *Nassarius* s.l., *Bullia* and *Buccinanops* are known. *Dorsanum* and *Cyllene* are rare but are known only from shallow-water.

Considering only the British species of the *Pseudocominella* group, it would seem unlikely that either *P. armata* or *P. deserta* was intertidal. The evidence in the case of the other species is not clear cut; any of them could well have been intertidal but there is no proof. Such a mode of life would help to explain the rather sporadic fossil record of the group; inshore deposits are relatively often eroded after deposition. The seas in which these forms lived would have been considerably warmer than those around Northern Europe now. At the present day the family is important in warmer waters, mostly within 40° North or South of the Equator. The occurrence of a few species of *Nassarius* s.l. in Northern European seas may be due to the warming influence of the Gulf Stream. Modern members of the family are carrion-eaters (Fretter & Graham, 1962 : 522).

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SYSTEMATIC DESCRIPTIONS

Order NEOGASTROPODA
Superfamily ***BUCCINACEA***
Family ***NASSARIIDAE***
PSEUDOCOMINELLA gen. nov.

(Pls 1–3; Pl. 4, figs 1–3)

Type species. *Buccinum desertum* Solander, 1766.

Diagnosis. Bucciniform; moderate sized, normally attaining an adult height of between 20 and 35 mm; protoconch of three convex, naticoid whorls; form of transition into teleoconch unknown; teleoconch of up to seven whorls; aperture broad, only slightly constricted anteriorly, about two-thirds height; posterior siphonal notch present; fasciole narrow, rugose and bounded adapically by a strong ridge and abapically by a strong fold and corresponding with a groove on the external shell surface; spiral ribbing on fasciole sometimes seen on juvenile shells; columella bent to the left and terminating in a raised diagonal plait abapically; columellar callus weak, often not quite obscuring ridge and fold of fasciole which may therefore appear as weak columellar plaits; outer lip usually spirally ribbed within, internal ribs unrelated to external ribs; growth lines wavy, essentially orthocline but bent adorally in sutural region and aborally to meet ridge of fasciole; weak sinus (stromboid notch) present in abapical part of outer lip; flat subsutural platform present; ramp concave; spiral ribbing fairly strong; collabral ribbing usually developed, with a tendency to become spinose at periphery.

Other species assigned. *Strepsidura armata* J. de C. Sowerby, 1850; *Buccinum bullatum* Philippi, 1847; *B. bullatum aspera* von Koenen, 1889; *Pseudocominella semicostata* nov. sp.; *Cominella solanderi* Cossmann, 1889.

Geological range. Middle Eocene (Lutetian) to Lower Oligocene (Lattorfian).

REMARKS. Vokes (1939 : 141) suggested that *'Cominella' deserta* might be congeneric with a group of species from the United States west coast Eocene, usually referred to *Siphonalia* (fam. Buccinidae). *S. bicarinata* Dickerson, in fact, strongly resembles both *P. armata* and *P. semicostata*. Its familial position is obscure. Like Recent *Siphonalia*, it possesses a very weak terminal columellar plait and reverse S-shaped growth lines on the fasciole. It is definitely not a *Pseudocominella*, which has a strongly grooved fasciole and an immediately obvious columellar plait. Some species of *Nassarius* (s.l.) have fairly similar apices and sculpture to *Pseudocominella*. They differ in often having a constriction of the neck above the fasciole whilst the fasciole itself may correspond with a convex fold which is often strongly spirally ribbed. The fasciole of *Strepsidura* (pl. 9, fig. 10) is similar to that of *Pseudocominella* but the former genus may be distinguished by its more twisted columella and by its aperture which is approximately four-fifths shell-height. In addition, its protoconch is larger and rather flattened apically. *Pseudocominella* differs from *Cominella* in the form of the fasciole and the lack of a columellar plait; the two genera are not co-familial.

Pseudocominella deserta (Solander, 1766)

(Pl. 1, figs 1–12)

1766 *Buccinum desertum* Solander: 13 (*pars*), pl. 1, fig. 15 (*non* figs 18, 19)
1823 *Buccinum desertum* Brander; J. de C. Sowerby: 14, pl. 415, fig. 1.
1850 *Fusus desertus* Morris; d'Orbigny: 363.
1854 *Buccinum excavatum* Beyrich: 444, pl. 10 (7), figs 1a, 1b, 1c.
1864 *Strepsidura deserta* (Solander) von Koenen: 100.
1866 *Buccinum* (*Cominella*) *desertum* Lowry *et al.*, pl. 3.
1880 *Cominella* (*Buccinum*) *deserta* (Solander) Judd: 154.
1881 *Cominella* (*Buccinum*) *deserta* (Solander); Keeping & Tawney: 116.
1888 *Buccinum desertum* Solander; Gardner, Keeping & Monckton: 626.
1889 *Buccinum desertum* Brander; Bristow *et al.*: 289.
1889 *Buccinum* (*Cominella*) *desertum* Sowerby; von Koenen: 241 (*pars*).
1889 *Cominella deserta* (Solander); Cossmann: 136 (*pars*).
1891 *Cominella deserta* (Solander); Newton: 168.
1901 *Cominella deserta* (Solander); Cossmann: 149, 150 (*pars*).
1901 *Cominella deserta* (Solander); Cossmann, pl. 6, fig. 4.
1933 *Cominella deserta* (Solander); St. J. Burton: 156.
1963 *Cominella deserta* (Solander); Glibert: 67 (*pars*).
1968 *Cominella deserta* (Solander); Martini & Ritzkowski: 244–247.

LECTOTYPE (designated herein). Upper Eocene, early Priabonian, Barton-on-Sea, Hants, figured Solander, 1766, pl. 1, fig. 15, GG 19667 (*Brander Colln.*).

PARALECTOTYPE (designated herein). GG 19668, same details, but not figured by Solander.

MATERIAL STUDIED. ENGLAND, Upper Eocene, early Priabonian, Barton Beds, coastal section between Highcliffe and Barton-on-Sea, Hants. Horizon not indicated: GG 19669/1 (figd. J. de C. Sowerby 1823, pl. 415, fig. 1, the central figure); GG 19670/1–25 (*Ed*). Lower Barton Beds, horizon A2, GG 19671 (*Ru*).

Horizon A3, GG 19672/1–3 (*Le*); GG 19673 (*S*); GG 19674/1–13 (*Wr*). Horizon B, GG 19675 (*Ru*). Middle Barton Beds, GG 19676/1–9 (*StJB*); GG 19676/1–6 (*Wr*). Horizon C, (*Je*); (*S*). Horizon E, (*Cu*); (*S*). Upper Barton Beds, Horizon H, GG 19678/1–3 (*Wr*); GG 1151 (*H. A. Toombs*); GG 19725 (*Cu*). Lower Barton Beds, Alum Bay, I.O.W., *Sand. Mus.* 3554 (*J. F. Jackson Colln.*); same (near top), GG 19732 (*Wr*). Upper Eocene, late Priabonian, Middle Headon Beds, Brockenhurst, GG 19679 (*Ed*). Brockenhurst Bed, Whitecliff Bay, I.O.W., *Sedg. Mus.* C 29122 (*K. & T.*). GERMANY, Upper Eocene, early Priabonian, Westeregeln, GG 19680/1–3 (*Ed*).

FURTHER OCCURRENCES. GERMANY, Westeregeln, (Beyrich, 1854 : 444; von Koenen, 1869 : 241; Glibert, 1963 : 67; Martini & Ritzkowski, 1968 : 244–247, with nannoflora indicating a similar age to that of the Upper Barton Beds (Bed H).

DIAGNOSIS. *Pseudocominella* up to 36 mm high; up to seven whorls of teleoconch; mean spire angle 55°–60°; prominent subsutural platform and concave ramp developed; spiral sculpture of narrow ridges often alternately of primary and secondary strength and separated by wide interspaces; collabral ribbing variable in strength and often rather irregular; outer lip ribbed internally; columellar callus developed.

DESCRIPTION. Each whorl is enveloped by the succeeding one just below the periphery. A prominent subsutural platform is developed on the third whorl (first of teleoconch) and reaches a width of 1·5 mm on specimens over 30 mm high. It is normally coronate, being crossed by the axial ribs; in axially multirugose specimens, however, it is often flat on later whorls. It is bordered by a collar bearing on later whorls up to three wavy spiral ribs (two on both the lectotype and paralectotype). The platform is undercut, the sutural ramp being noticeably concave. The whorl shoulder is distinctly adapical to the periphery. On the first and second whorl of the teleoconch one spiral rib marks the margin of the subsutural platform, another the shoulder, and three or four more lie on the rather flat abapical portion of the whorl. These ribs are broad, rather flattened in section, and are separated by narrow grooves. On the third whorl the interspaces broaden and spiral ribs of secondary strength may appear, first on the sutural ramp, then between the primary rib marking the shoulder and the one immediately abapical to it. On later whorls five or six primary spiral ribs of intermediate strength may be distinguished on the increasingly convexly-sided portion of the whorl abapical to the shoulder. These ribs are narrow and are separated by interspaces about double their width. Secondary and sometimes tertiary ribs are often developed with no discernible pattern. On the body whorl between fifteen and twenty-two primary ribs are developed between the shoulder and the adapical margin of the fasciole; up to twenty-five ribs of secondary and tertiary strength may also be present in the same area. On the lectotype there are fifteen primary and fifteen secondary ribs in this region. In the same region there are thirty-nine ribs on the paralectotype but it is difficult to separate them into different orders of strength. The first whorl of the teleoconch bears about thirteen collabral ribs which are well-rounded in section. On the next two whorls the number increases to between fifteen and twenty-five and thereafter remains fairly constant on all succeeding whorls. The lectotype is a particularly multicostate specimen (see table). The spacing and strength of the collabral ribs often varies on a particular shell as well as between different ones. Their strength is normally inversely proportionate to their number. They are strongest at the shoulder which is often slightly nodose. The ribs are usually weaker on the subsutural ramp but stronger on the subsutural platform. They decrease in strength below the periphery. A variable number of internal spiral ribs occur on the inner surface of the outer lip. They are rather irregularly arranged, stretch back into the aperture for varying distances, and some are discontinuous.

DIMENSIONS	1	2	3	4	5	7	8	9	10	11
GG 19667 LT	26·8	14·1	15·6	6+	25	30	9	23	1·90	1·72
GG 19668 PLT	22	13·4	14·1	6	11+	39	13	19	1·64	1·56
GG 19671	8·8	5·3	5·0	4½	12	23	6	15	1·66	1·76
GG 19672/1	12·6	7·4	7·2	5	20	29	11	16	1·70	1·75
GG 19673/1	17·1	10·3	9·4	5½	0	36	11	14	1·66	1·82
GG 19677/11	22·9	12·7	13·2	6	15	36	9	21	1·80	1·74
GG 19677/1	30·9	15	16·5	6½	14	26	11	16	2·06	1·87
GG 19670/5	34·1	19·2	19·6	7	15+	32	15+	—	1·77	1·74

Key (also used in all following descriptions)
HT, Holotype; LT, Lectotype; NT, Neotype; PLT, paralectotype; PT, paratype.
1, total height (mm)
2, height of aperture
3, breadth
4, number of teleoconch whorls
5, number of collabral ribs on last whorl
6, number of collabral ribs on penultimate whorl (not shown for this species)
7, number of spiral ribs on last whorl
8, number of spiral ribs on penultimate whorl
9, number of spiral ribs inside outer lip
10, height: height of aperture
11, height: breadth

REMARKS. *Buccinum fusiforme* Deshayes, from the Lutetian and Auversian of the Paris Basin, was placed in the synonymy of this species by Cossmann (1889 : 136). A re-examination of Deshayes' specimens in the École des Mines (see p. 195) shows that they all clearly belong to *P. armata*. All subsequent continental authors, however, have accepted Cossmann's views. In the synonymy given here it is assumed that their records of French specimens are of *P. armata* and not of *P. deserta*, and that *P. deserta* does not occur in France.

From examining the lectotype and paralectotype it would appear that other authors have correctly interpreted English specimens of the species. The other specimens figured by Solander (pl. 1, figs 18, 19) as *Buccinum desertum* are both lost. J. de C. Sowerby (1823, pl. 415, fig. 2) thought that Solander's fig. 18, and possibly fig. 19 belonged to his new species *Buccinum canaliculatum* (now *Bartonia* see p. 181); these determinations have since been disputed. Cossmann (1889 : 137) identified Solander's figure 18 as *Cominella deserta* var. *solanderi* (Edwards MS). D. Curry (personal communication) points out that Solander's fig. 19 is much more likely to be of *Buccinum lavatum* J. de C Sowerby (now *Pollia*).

In the adult stage *P. deserta* most clearly resembles *P. bullata* (Philippi) (pl. 2, figs 9a, b) from the Lower Oligocene of Latdorf, Germany. The whorl profile of the latter is more evenly convex, the subsutural ramp being barely grooved. Its sculpture, particularly the collabral elements, is weaker, and the first four whorls of the teleoconch are much smoother. In some specimens the collabral ribs on the last body whorl are relatively strong in the peripheral region where they form definite nodes. The spiral ribs on the inner surface of the outer lip are more numerous. Comparisons with *P. armata* and *P. solanderi* are discussed under the latter named.

The records by Morris (1843 : 146) from Bracklesham (as *Fusus desertus* Brander), by Forbes (1856 : 86) from the Headon Beds of Colwell Bay and by Nyst (1836 : 36) from the Tongrian of Klein Spauwen (Belgium) cannot be confirmed and are almost certainly incorrect. Bristow *et al.* (1889 : 289) erroneously state that Keeping & Tawney (1881) record this species from the Bracklesham Beds of the Isle of Wight. This record, in fact, is from the Brockenhurst Bed of the Headon Series (see 'Material Studied').

Giebel (1864 : 17, pl 1, fig 1) described and figured *Buccinum bullatum* Philippi from Latdorf. Von Koenen (1865 : 466) redetermined this as *Strepsidura deserta* (Solander) From the figure it is clear that Giebel's determination was right and von Koenen's was wrong. In his more authoritative later publication (1889 : 241) von Koenen does not record *P. deserta* from Latdorf.

Pseudocominella armata (J. de C. Sowerby, 1850)

(Pl. 3, figs 1–8)

1835 *Buccinum fusiforme* Deshayes: 653.
1837 *Buccinum fusiforme* Deshayes; Deshayes, pl. 87, figs 15, 16, 17.
1850 *Buccinum fusiforme* Deshayes: d'Orbigny: 420.
1850 *Strepsidura armata* J. de C. Sowerby *in* Dixon: 104, 186, pl. 7, fig. 11.
1865 *Buccinum fusiopsis* Deshayes: 499.
1889 *Cominella deserta* (Solander) Cossmann: 136 (*pars*).
1891 *Strepsidura armata* J. de C. Sowerby; Newton: 165 (*pars*).
1901 *Cominella deserta* (Solander); Cossmann: 149, 150, (*pars*).
1911 *Cominella deserta* (Solander); Cossmann & Pissarro, pl. 37, fig. 178–1.
1948 *Cominella deserta* (Solander); Morellet, L. & J.: 30, 133, 179, 331, 343.
1963 *Cominella deserta* (Solander); Glibert: 67 (*pars*).

NEOTYPE (proposed herein). Middle Eocene, Auversian, exact horizon unknown, (probably Bed 19 (Brook Bed) of Fisher 1862 : 74) Upper Bracklesham Beds, Bracklesham Bay, Sussex, GG 19681/1 (*Ed*).

MATERIAL STUDIED. ENGLAND, All from Upper Bracklesham Beds, Auversian. Bracklesham Bay, GG 19681/2–4 (*Ed*) (probably same horizon as Neotype); G 8869/1–6 (*Ogle Colln.*); Bed 19 (Brook Bed) of Fisher (1862 : 74), *Sedg. Mus.* C 64860 (*Fisher Colln.*); G 75897, G 75998 (*E. M. Venables Colln.*). Brook, Hampshire GG 19683/1–4 (*Ed*); *Sedg. Mus.* C 67793. Huntingbridge, Hampshire, GG 19684 (*Ed*). Bramshaw, Hampshire, GG 19685/1–4 (*Ed*). 'Fossil bed' at Bramshaw of Fisher (1862 : 81, lines 2–4), 1 juvenile (*Cu*). FRANCE, Two separate samples in Deshayes

Colln., École des Mines, Paris (see p. 195). One labelled Le Fayel, Mary and Caumont, the other labelled Vendrest, Auvers and Acy, with no indication as to which shell comes from which locality. All these localities were quoted by Deshayes (1865 : 499), none of them were mentioned by him in his original description (1835 : 653–654).

Further occurrences. France, Lutetian:—Grignon (Deshayes, 1835 : 654), (Cossmann 1889 : 137). Auversian: Valmondois (Deshayes 1835 : 654) (1865 : 499); Le Guépelle (Deshayes, 1865 : 499); Bezu-le-Guery, Le Fayel (Glibert, 1963 : 67); Auvers (p. 133), Nanteuil-le Haudouin (p. 179), Acy (p. 331), Ru d'Alland valley (p. 343) Morellet (1948); Acy (Cossmann & Pissarro, 1911, pl. 37, fig. 178–1). Exact horizon unknown. Senlis (Deshayes, 1835 : 654).

Diagnosis. *Pseudocominella* with teleoconch of up to six whorls; mean spire angle between 60° and 65°; up to twenty-five collabral ribs per whorl on early part of teleoconch, reducing to about ten increasingly nodose ribs on each of the last two to three whorls; whorl profile convex on early whorls, shoulder becoming increasingly angular on later whorls; spiral sculpture of varying strength; margins of fasciole strongly ridged; fasciole very rugose; outer lip denticulate within in some individuals.

Description. All the specimens are damaged and those from the type locality are partly crushed. The protoconch (pl. 3, fig. 4) is typical for the genus and is fairly well-preserved on specimens from Brook and Bramshaw. It consists of about three apparently smooth naticoid whorls. The subsutural platform and close-set collabral ribbing first appear towards the end of the third whorl. On the first three or four whorls of the teleoconch the subsutural platform is bordered by a raised rim which eventually becomes obsolete, finally, on the body whorl the platform tends to be downward sloping. The early whorls of the teleoconch are broadest at the adapical suture and are evenly convex in profile except for a groove under the subsutural platform. In later whorls this groove develops into a broad concave ramp. The profile is further modified by the development of nodes at the shoulder, below which the whorl-sides are vertical.

The two strongest spiral ribs on the early teleoconch mark the edge of the subsutural platform and the shoulder. On later whorls there are normally two strong ribs in each of these positions. They are joined by others on the ramp itself and increase in number to between seven and fifteen on the ramp of the last whorl. The spiral sculpture differs considerably on specimens from different localities. The patterns of ribbing on the ramp of shells from Bracklesham Bay, Whitecliff Bay and Brook are similar; Bramshaw and Huntingbridge shells differ in having much stronger ribs which may be differentiated into those of primary and secondary strength. Below the shoulder on the peripheral region, up to ten weak spiral ribs may be seen with difficulty on the spire whorls of specimens from Bracklesham Bay. These usually die out on the body whorl of Bracklesham specimens (including the neotype) but always persist on specimens from other localities. The ribs are barely stronger on the Whitecliff Bay and Brook specimens. The Bramshaw and Huntingbridge shells have over forty considerably stronger and more clear-cut ribs of both primary and secondary strength on the body whorl. The neck region of specimens from all localities bears between eleven and fifteen spiral ribs.

There are between twenty and twenty-five collabral ribs on each of the first two whorls of the teleoconch. These become more irregular in strength and spacing on the next whorls, reducing eventually in number to about nine evenly spaced nodes on the fifth and sixth whorl of the teleoconch. On the earlier whorls they are well-rounded in section, separated by rather broader, smoothly concave interspaces. They are moderately strong and of even strength below the shoulder; above it they markedly decrease in strength and are almost obsolete at the sub-sutural ramp. On the body whorl the collabral sculpture is confined to the area just above and below the shoulder. It consists of strong nodes or sometimes blunt spines. Six of the twelve specimens from the type locality have, on the last whorl, indications of a growth halt during which an aperture similar to the terminal one was developed. Here, the growth lines are more prominent, the outer lip was apparently slightly flared and parietal callus remains above the adapical suture of the previous whorl. One specimen has two such halts and on two of the larger shells these halts occur about 180° before the terminal aperture. Signs of preterminal apertures are common but much less prominent on specimens from other localities. The track of the fasciole is rather deeply grooved, and its bordering ridges, particularly the anterior, are strong. Growth rugae in this region are noticeably imbricate especially in the larger shells. The aperture is damaged in all specimens; none of those from the type locality and only one out of the four from Brook shows any indications of the outer lip being denticulate within. Internal ribs stretch back for about 45° within the aperture in specimens from other localities. In one specimen from Bramshaw these break down into numerous intermittent dashes as the aperture is approached.

DIMENSIONS.	1	2	3	4	5	6	9	10	11
GG 19681/1 NT	25·5	15·7	16±	6	9	10	—	1·6	1·57
GG 19681/2	22+	—	15·1	6	10	10	—	—	1·47
GG 19681/3	22	13	12·9	6	9	12	—	1·69	1·70
GG 19681/4	17+	11±	10·3	6	8	10	—	—	—
GG 19685/4	12	7	6·5	5+	13	18	—	1·71	1·84
GG 19685/3	16	9·2	9·7	5+	12	19	12	1·74	1·65
GG 19685/1	26·7	16·2	16·7	6+	9	9	15	1·65	1·60
GG 19685/2	28+	16·5	17·7	6+	10	9	some	1·70	1·58
GG 19684	15·5	9·3	9·3	6	9	12	13	1·67	1·67

(see p. 192 for key)

REMARKS. The appearance and matrix of the neotype and associated specimens GG 19681/1–6 (*Ed*) matches that of the specimens listed which are known to come from the Bed 19 (The Brook Bed) at Bracklesham Bay.

All the French records of '*Cominella*' *deserta* are considered herein to be of *P. armata* (see pp. 192 and 194). Specimens of *Buccinum fusiopsis* in the Deshayes Collection (*EMP*) (no specimens from Deshayes original (1835: 653–654) localities survive) and the specimen from Acy figured as *Cominella deserta* by Cossmann and Pissarro (1911, pl. 37, fig. 178–1) have strong sculpture very similar in character to that of specimens from Bramshaw and Huntingbridge in the New Forest (Hampshire). The specimen which Cossmann figures (1901, pl. 6, fig. 4) as *Cominella deserta* is stated to be from Barton and the specific identification appears to be correct. All the English specimens of *P. armata* have stronger nodes at the periphery of the last whorl than any of the French specimens examined; the closest comparison is between them and the specimen figured from Huntingbridge (cf. pl. 3, figs 6 and 8). *P. deserta* always has a more rounded whorl profile and a narrower, more concave ramp. The only previous figure of an English specimen of the species is of the relatively smooth form originally described by Sowerby from Bracklesham Bay (1850, pl. 7, fig. 11). Without knowledge of the Bramshaw and Huntingbridge specimens, it is hardly surprising that French authorities considered their specimens either to be specifically distinct from *P. armata* or to be synonymous with *P. deserta*. The exposures at Bramshaw and Huntingbridge are slightly younger than the Brook Bed (Bed 19) of Brook and of Bracklesham Bay (Fisher, 1862 : 92–93; Curry 1958 : 70–71). It seems likely that *P. armata* gave rise to *P. deserta*. Changes include an increase in strength of spiral sculpture, an increase in the number of collabral ribs on the later whorls, gradual disappearance of peripheral nodes and the narrowing of the ramp.

Deshayes proposed the name *Buccinum fusiopsis* (1865 : 499) as his earlier name *B. fusiforme* (1835 : 653) was preoccupied (Borson, 1820 : 222). Sowerby's name (1850 : 104, 186) therefore stands. The surviving parts of both Dixon's and the Sowerby family's collections are housed in the British Museum (Natural History), but the whereabouts of this figured specimen is unknown. Comparisons with *P. deserta* and *P. solanderi* follow the description of the latter, whilst those with *P. bullata* (Philippi) and *P. semicostata* are discussed under the last named. The name *armata* has often been applied erroneously to *P. semicostata* (see its synonymy). The record from the Belgian Oligocene by Glibert & de Heinzelin (1954 : 367) of *Northia* (*Cominella*) *bullata* f. *armata* is of *P. bullata*.

Pseudocominella semicostata sp. nov.

(Pl. 3, figs 9–10; Pl. 4, figs 1–3)

1864 *Strepsidura deserta* var. *armata* J. de C. Sowerby; von Koenen: 100.
1880 *Strepsidura* (*Buccinum*) *armata* J. de C. Sowerby; Judd: 154.
1880 *Strepsidura* (*Buccinum*) *semicostata* Edwards MS; Judd: 154 (*nom. nud.*).
1881 *Strepsidura* (*Buccinum*) *armata* J. de C. Sowerby: Keeping & Tawney: 111, 113, 116.
1881 *Strepsidura* (*Buccinum*) *semicostata* Edwards MS; Keeping & Tawney: 116 (*nom. nud.*).
1882 *Strepsidura armata* J. de C. Sowerby; Judd: 477.
1891 *Strepsidura armata* J. de C. Sowerby: Newton (*pars*): 165.
1891 *Strepsidura semicostata* Edwards MS; Newton: 165 (*nom. nud.*).
1901 *Strepsidura armata* J. de C. Sowerby; Cossmann: 133.
1901 *Strepsidura semicostata* Edwards MS; Cossmann: 133 (*nom. nud.*).
1902 *Strepsidura armata* J. de C. Sowerby; Reid: 40.
1915 *Strepsidura armata* J. de C. Sowerby; White: 44.
1926 *Melongena* (*Cornulina*) *minax* (Solander) Jackson: 360 (*pars*).
1926 *Strepsidura armata* J. de C. Sowerby; Jackson: 364.
1960 *Strepsidura armata* J. de C. Sowerby; Glibert: 9.

HOLOTYPE. Upper Eocene, Late Priabonian, Middle Headon Beds, Whitley Ridge, railway cutting, Brockenhurst, Hampshire GG 19687/1 (*Ed* ex *K*).

PARATYPES. All Upper Eocene, Late Priabonian, Middle Headon Beds. Whitley Ridge Railway cutting, Brockenhurst, Hampshire, GG 19687/2–3 (*Ed* ex *K*); *Sedg. Mus.* C 26453–8 (*K*). Victoria Tilery, Brockenhurst, (*S*). 'Brockenhurst', exact locality unknown, GG 19688/1–14 (*Ed*); GG 19689/1–2 (*StJB*); G 7760 (*Beckles Colln.*). Lyndhurst, Hampshire, GG 19690/1–4 (*Ed*). Royden, Hampshire GG 19686/1–9 (*Ed* ex *K*); *Sedg. Mus.* C 25070–90 (*K&T*). Brockenhurst Bed, Whitecliff Bay, I.O.W., GG 19692/1–5 (*Wr*); *Sedg. Mus.* C 29270–3 (*K&T*); *Sand. Mus.* 1930 (*J. F. Jackson*), recorded as *Melongena minax*. *?Venus Bed*, Colwell Bay, I.O.W., GG 19691 (*Ed*).

FURTHER OCCURRENCES. Unknown.

DIAGNOSIS. Stout *Pseudocominella* with between six and seven whorls of teleoconch; mean spiral angle increasing from 60° to 80° with growth; ramp broad; shoulder angular except for early teleoconch, low, at or below mid-height of spire whorls; about twenty-one collabral ribs on early part of teleoconch reducing to nine or ten very nodose ribs on last three whorls; aperture broad; fasciole bordered by strong ridges; fasciole very rugose; outer lip denticulate within in some specimens.

DESCRIPTION. The protoconch is decorticated or missing in all specimens; its gross size and shape is similar to that of *P. deserta* (Solander). The first two to three whorls of the teleoconch are broadest at the adapical suture and are convex in profile except for a subsutural constriction which rapidly grows into a broad concave ramp. The profile becomes strongly carinate on the fifth and sixth whorl of the teleoconch, with the periphery coinciding with the shoulder. The subsutural platform is horizontal, on later whorls it becomes wavy under the influence of the axial nodes. At the earliest point in the development of the teleoconch at which it is possible to determine detail there are three prominent spiral ribs, and the whorl profile is naticoid. During this whorl, two new ribs develop between the two most adapical. The opisthocyrt collabral costae are of similar strength and form a reticulate pattern with slight nodes at the intersections; they do not extend on to the subsutural platform which first develops on this whorl and is bordered by a spiral rib. The following whorl (third of the teleoconch) is similar except for the broadening of the subsutural ramp which lacks spiral ribbing. The shoulder is marked by the second most adapical spiral rib. The reticulate pattern is made of increasingly spirally-elongate rectangles. On the fourth teleoconch whorl the increasing strength of the collabral ribs compared with the spiral ribs becomes noticeable; within the next whorl or so this leads to the loss of the reticulate appearance. The ramp gradually becomes concave and bears two new spiral ribs of secondary strength. The edge of the subsutural platform is marked by two strong spiral ribs and another pair lies on the shoulder. Between the fifth and seventh teleoconch whorls seven to ten spiral ribs are developed on the ramp. Apart from those on the shoulder and bordering the subsutural platform these are seldom of greater strength than those on earlier whorls and are often difficult to follow even on well-preserved shells. On immature specimens with a teleoconch of four whorls, there are on the body whorl between eighteen and twenty spiral ribs of varying strength below the shoulder, seven or eight of these being on the neck and rather stronger. The full adult number of spiral ribs, about twenty-nine in all, of which fourteen are on the neck, is reached by the sixth teleoconch whorl. There are between eighteen and twenty-one collabral ribs on the first four teleoconch whorls; these die away below the peripheral region of the body whorl even in juvenile shells. On the next whorl these weaken on the ramp and become increasingly nodose at the shoulder and grow further apart. From here on nine or ten axial nodes or spines occur on each whorl. The fasciole is strongly ridged and is very rugose in large specimens. Specimens showing ribs on the inside of the outer lip are very rare.

DIMENSIONS.	1	2	3	4	5	6	7	8	9	10	11
GG 19687/1 HT											
estimated	27·0	—	—	—	—	—	—	—	—	1·86	1·52
actual	26·1	14·5	17·8	6	13	12	—	—	16	—	—
GG 19686/2 PT	20·3	12·8	13·7	5½	9	11	36	12	10	1·58	1·48
GG 19686/3 PT	13·8	8·5	8·5	5	12	21	33	10	0	1·62	1·62
GG 19686/4 PT	8·7	5·5	5·2	4½	16	20	23	7	11	1·58	1·67
GG 19686/5 PT	7·4	4·7	4·3	4	—	17	28	5	0	1·57	1·72
GG 19688/1 PT	32+	19·5	21·1	6½	8	12	42	—	0	—	—

(see p. 192 for key)

REMARKS. Edwards gave the manuscript name *Strepsidura semicostata* to his single specimen from Colwell Bay (GG 19691). This was so badly worn that he failed to recognize that it was conspecific with numerous other specimens (listed here) which he identified as *S. armata*. *P. semicostata* differs from *P. armata* in being relatively stouter, having a broader, less sloping ramp, more prominent axial nodes, and a lower shoulder. It has also been confused by von Koenen (1864 : 100) and by Judd (1880 : 154) with *P. bullata* (Philippi) which may be easily distinguished by its much weaker collabral sculpture on the early teleoconch; strong axial ribbing and nodes are normally confined to its body whorl.

Pseudocominella solanderi (Cossmann, 1889)

(Pl. 2, figs 1–8)

1766 *Buccinum desertum* Solander: 13 (*pars*), pl. 1, fig. 18 (*non* figs 15, 19).
1887 *Cominella solandri* Edwards; Keeping: 71 (*nom. nud.*).
1888 *Buccinum solandri* Gardner, Keeping & Monckton: 620 (*nom. nud.*).
1888 *Buccinum* sp. nov.; Gardner, Keeping & Monckton: 627.
1889 *Cominella solandri* Edwards; Bristow: 120, 290 (*nom. nud.*).
1889 *Cominella deserta* (Solander) var. *solanderi* Edwards; Cossmann: 137.
1901 *Cominella* (*Buccinum*) *solanderi* (Edwards) Cossmann: 150.
1926 *Cominella solandri* Edwards MS; Jackson: 356.
1933 *Cominella* sp.; Burton: 156.

NEOTYPE (selected herein). Upper Eocene, early Priabonian, Lower Barton Beds, Horizon A3, coastal section between Highcliffe and Barton, Hampshire, GG 19693/1 (*Ho*).

MATERIAL STUDIED. Same locality, Lower Barton Beds, horizon unspecified GG 19696/1–20 (*Ed*); 19697/1–10 (*Wr*). Horizon A2, GG 19703 (*Ru*). Horizon A2 (near top) GG 19698/1–20 (*Nu*). Horizon A3, GG 19699/1–50 (*S*); GG 19700/1–3 (*StJB*); GG 19693/2–3 (*Ho*); GG 19694/1–18 (*Le*); GG 19695/1–3 (*S*); (*Cu*); (*Je*). Horizon B, 2 specimens (*Ru*).

Alum Bay, I.O.W., Barton Beds, horizon unknown, *Sedg. Mus.* C 59712–4; (10 specimens) *Sand. Mus.* 4720. Lower Barton Beds (near top) GG 19731/1–8 (*Wr*); (2 specimens) *Sand. Mus.* 1084 (*J. F. Jackson Colln.*). Whitecliff Bay, I.O.W. Barton Beds, lowest 13 inches with *Nummulites elegans*, *Sedg. Mus.* C 64098 (*K*).

FURTHER OCCURRENCES. Lower Barton Beds, Barton-on-Sea, as *Cominella* sp., horizons A3 and B (Burton, 1933 : 156).

DIAGNOSIS. Moderate sized, fairly elongate *Pseudocominella* with a marked horizontal and undercut subsutural platform; mean spire angle between 50° and 60°; collabral ribs present only on early whorls of neoconch; spiral sculpture of close-spaced low ribs; outer lip ribbed internally.

DESCRIPTION. The protoconch is about 1·2 mm high and broad. Its first half whorl is minute; it seems to be disjunct with a semi-erect tip, but this appearance is certainly due to weathering. It is followed by two and a half smooth naticoid whorls. It seems very unlikely that the transition to the teleoconch was abrupt; orthocline collabral ribs of increasing strength occur, these soon become nodose and are joined by spiral ribbing within a quarter whorl. Most adult specimens are badly worn; the sculpture of the body whorl is abraded and the early whorls either decorticated or even missing, the main exceptions are immature specimens under 8 mm high. Teleoconchs of shells 20 mm high would have been of six whorls. Each whorl is enveloped by the succeeding one just below the periphery. The first two-and-a-half to three teleoconch whorls bear twelve, increasing to sixteen rather angular, orthocline, collabral ribs. These die out by a shell height of between 6 and 8 mm, except on a very few of the specimens seen, where they persist above the periphery sometimes until full growth is reached. On succeeding whorls the only collabral sculptural elements are rugae which are distinctly stronger than the growth lines seen on well preserved shells. Spiral ribbing and the subsutural platform appear about a quarter whorl after the first collabral ribs. The subsutural platform, which reaches a width of 1 mm on the last whorl of large shells is normally horizontal but may slope either upwards or downwards away from the suture. Another fairly strong spiral rib marks the shoulder, which is nodose and carinate for the first two or three whorls of the teleconch. Within the next two whorls these are joined by a weaker spiral rib on the concavely-sloped sutural ramp and three or four more between the shoulder and the suture below. By the fifth teleoconch whorl the latter have increased in number to eight or nine. Two spiral ribs of lower strength commonly occur on the sutural ramp. On the last whorl other weak ribs are sometimes irregularly disposed, mainly above the periphery. The number of spiral ribs on the last whorl increases with size (see table), most adult shells having between thirty-eight and forty ribs of varying strength. The nine or ten on the neck region are the strongest, apart from the primary ribs on the shoulder and on the edge of the subsutural platform. The spiral ribs are about the same width as the interspaces except on the neck region where they are more widely spaced. In section they are usually gently convex and often almost flat-topped. The inner surface of the outer lip bears ribs which do not correspond with the external ones. They stretch back inside the aperture for nearly a quarter whorl in large individuals, less so in small ones and are resorbed as the shell grows. The number of internal ribs is about half that found on the outer surface and is dependent on size. Two spiral colour-bands may be seen on the neotype, one, about a millimetre broad, on the ramp with a narrower one just below the shoulder, other specimens also show this phenomenon (pl. 2, figs 4, 6, 7, 9).

DIMENSIONS.	1	2	3	4	5	6	7	8	9	10	11
GG 19693/1 NT	14·7	7·6	7·8	5½	0	0	28	10	18	1·93	1·89
GG 19695/3	5·2	3·0	2·9	3	19	14	17	5	13	1·73	1·79
GG 19694/17	6·2	3·5	3·5	4	9	16	24	7	11	1·77	1·77
GG 19693/2	8·6	4·7	4·5	4½	0	14	25	10	11	1·83	1·91
GG 19694/14	10·8	6·1	6·5	5	6	15	32+	11	14	1·72	1·66
GG 19694/10	12·6	7·4	6·8	5	0	0	38+	11	17	1·70	1·61
GG 19694/6	14·6	8·2	8·2	5	4	15	41	14	17	1·78	1·78
GG 19694/5	17·8	9·5	9·2	5½	0	0	35	19	19	1·87	1·93
GG 19694/1	20·0	12·0	11·1	6	0	15	41	16	22	1·67	1·80
GG 19700/3	25·5	13·5	13·8	—	0	—	—	—	20	1·89	1·85

(see p. 192 for key)

REMARKS. Cossmann (1889 : 137) in discussing *P. deserta* wrote 'les figures qu'en donne Brander sont très exactes, sauf la figure 18, qui représente une variété pour laquelle a été proposé le nom *Solanderi*, Edw.'. The specimen figured by Solander is lost. None of the specimens GG 19696/1–20 in the Edwards Collection, which are labelled as *solandri*, have been chosen as neotype as they are all badly worn. In the circumstances it seems justifiable to select a neotype from better preserved material whose horizon is known more precisely.

This species is unknown except from the Lower Barton Beds. One sample, GG 19701/1–4 (*Wr*) was labelled as being from the Middle Barton Beds. Examination by several workers suggested that the specimens did in fact, come from the Lower Barton Beds. Moreover glue was present on the specimens, unlike others in Wrigley's Collection, suggesting that he might have acquired the specimens from an old collection and had assumed that any information with the specimens was correct. Another specimen, GG 19702 (*Wr*) was found in the same box as three specimens of *P. deserta*, GG 19678/1–3 (*Wr*) from the Upper Barton *Chama* Bed (Bed H). Again, examination by several workers showed that the preservation and matrix of the specimen of *P. solanderi* was not the same as that of its companions and that it was almost certainly from the Lower Barton Beds.

This species is among the twenty most common prosobranchs in horizon A3, of the Lower Barton Beds where *P. deserta* is extremely rare. The latter species, however, is more common in the Middle and Upper Barton Beds in which *P. solanderi* is unknown. Both species usually attain a height of 20 mm in Bed A3 of the Lower Barton Beds. In the Middle Barton Beds, *P. deserta* often exceeds 30 mm in height. This increase in size corresponds with almost an extra whorl (making a total of seven for the teleoconch).

P. deserta is relatively broader and its sculpture is stronger. The spiral sculpture is the only completely consistent difference between the two species. In *P. deserta* the interspaces are wider and the ribs are usually alternately of primary and secondary strength. A small proportion of specimens of one species may show one or more of the features listed below which normally distinguish it from the other. In *P. deserta* the collabral ribs tend to increase in strength with size, whilst they become obsolete by the third whorl in all but a few *P. solanderi*. The subsutural platform is broader and more strongly grooved below in *P. deserta* and the carina on the shoulder persists to adulthood in most individuals.

In all four of the British species of *Pseudocominella*, the early teleoconch has such similar sculpture, shape and rate of whorl expansion that juveniles are difficult to tell apart. The nodiferous, carinate, shoulder of this stage is most noticeable and of shortest duration in *P. solanderi* which is the least strongly sculptured when adult.

DESORINASSA gen. nov.

(Pl. 4, figs 4–9, Pl. 5, figs 1–5)

TYPE SPECIES. *Buccinum desori* Deshayes, 1865.

DIAGNOSIS. Agrees with *Pseudocominella* except in the following respects: subsutural platform not always developed; sculpture very weak; columella curved to the right above columellar plait; growth lines of fasciole not particularly rugose and not very sinuous; ridge above fasciole not strong; outer lip smooth within.

OTHER SPECIES ASSIGNED. **Buccinum acies* Watelet, 1853 (*IRScNB*); ***Cominella bonnecarrei* Furon 1948; **Buccinum latum* Deshayes, 1865 (*EMP*); *Buccinum ovatum* Deshayes 1835 (*EMP, MNP*). ***Cominella supracostata* Traub, 1938; **Desorinassa williamsi* sp. nov. (see footnote for explanation).

GEOLOGICAL RANGE. Palaeocene (Thanetian) to Lower Eocene (Cuisian).

REMARKS. *Desorinassa* may be distinguished from *Pseudocominella* by its curved columella and its weaker sculpture, in particular the almost complete lack of collabral elements. The fasciole is more like that of *Keepingia* and *Thanetinassa*.

The specimens of *Buccinum latum* Deshayes, (*Deshayes Colln., EMP*) figured herein as pl. 4, fig. 8 and pl. 4, fig. 9 are selected respectively as LECTOTYPE, and PARALECTOTYPE of this species. They are labelled as being from Abbecourt and Bracheux with no indication as to which specimen comes from which locality. These are the only localities quoted by Deshayes in his original description (1865 :

In these lists * denotes species in which the protoconch has not been studied, ** denotes that no specimens have been examined.

501). It would appear that his illustration of the apertural view of the species (1866, pl. 93, fig. 27) is composed of the outline of the lectotype upon which has been superimposed the better preserved outer lip and stronger columellar and parietal callus of the paralectotype.

Desorinassa desori (Deshayes, 1865)

(Pl. 4, figs 4–6)

1865 *Buccinum desori* Deshayes; 501.
1866 *Buccinum desori* Deshayes; Deshayes, pl. 93, figs 16, 17.
1889 *Cominella desori* (Deshayes) Cossmann: 137.
1901 *Cominella desori* (Deshayes); Cossmann: 150.
1911 *Cominella desori* (Deshayes); Cossmann & Pissaro, pl. 37, fig. 178–3.
1934 *Cominella desori* (Deshayes); Cooper: 8.
1936 *Cominella desori* (Deshayes); Farchad: 22.
1963 *Cominella desori* (Deshayes); Glibert: 67.

MATERIAL STUDIED. ENGLAND, Palaeocene, Thanetian, Thanet Sand, Reculver, Kent GG 19704 (*Wr*) (see remarks p. 203). FRANCE, Thanetian, Jonchery-sur-Vesle, France, GG 19705/1–3 (*Wr*); G 19438/1, 2 (*L. Staadt*).

FURTHER OCCURRENCES. ENGLAND, Thanetian, Bishopstone, near Reculver, (Cooper, 1934 : 8) (see remarks, p. 203). FRANCE, 'Sables inferieurs' (= Thanetian), Abbecourt; Châlons-sur-Vesle; Jonchery; Saint Martin-aux-Bois (Deshayes, 1865 : 501). Châlons; Chenay; Jonchery; Noailles (Glibert 1963 : 67). Bracheux, near Beauvais (Farchad, 1926 : 22).

DIAGNOSIS. Moderately large, stout, almost smooth *Desorinassa* with broad, sloping subsutural platform; mean spire angle about 60°; sutural slope reversed just prior to adult aperture; ridge on adapical side of fasciole very weak; outer lip not striate within.

DESCRIPTION. The protoconch is worn but appears to have been similar to that of *Pseudocominella*, consisting of about three smooth, naticoid whorls; initially it may have been somewhat flattened. The teleoconch has up to six whorls which are convex-sided with the periphery lying just above the suture. A cord may be seen below the suture on the first whorl of the teleoconch. The material is not well enough preserved to show the development of the subsutural platform. It is first recognizable by the third whorl of the teleoconch where either two (or in some specimens three) spiral ribs, situated high on the ramp near the suture, form an angulation in the whorl profile. Subsequently the platform becomes flatter, though the slope is never less than 45°. It reaches a breadth of nearly 1·5 mm. No groove is developed but the profile is slightly concave just below the platform. Spiral sculpture is poorly developed, there are two or three weak grooves just below the subsutural platform and a mixture of about fifteen weak grooves and step-like ribs on the neck region of the body whorl. Collabral sculpture is absent except for growth rugae, these are strongest away from the periphery, becoming quite noticeable on and just below the subsutural platform and to a lesser extent on the neck region. The ridge marking the adapical margin of the fasciole can hardly be distinguished in smaller specimens. No ribbing has been seen inside the outer lip. The sutural slope becomes reversed immediately prior to the final aperture.

DIMENSIONS.	1	2	3	4	7	10	11
GG 19704	22+	11+	14+	—	—	—	—
GG 19705/3	11·3	6·5	6·3	4+	12+	1·74	1·79
GG 19705/1	13·3	8·2	7·9	4½	17+	1·62	1·68
G 19438/2	16·5	9·9	9·7	—	—	1·67	1·70
G 19438/1	17·6	10·0	10·6	5+	18+	1·76	1·66

(see p. 192 for explanation)

REMARKS. *D. desori* differs from *D. acies* (Watelet) (pl. 5 fig. 5) and *D. ovata* (Deshayes) (pl. 5, fig. 4) in being larger, having a subsutural platform and lacking regular spiral sculpture. A comparison with *D. williamsi* is given under the latter. The single English specimen of *D. desori* seen is badly damaged but agrees in all essential respects with the French specimens.

It is thought that Wrigley acquired many of the more interesting specimens of J. E. Cooper's collection and GG 19704 was found in a box which was probably made by Cooper. It is therefore possible that this specimen is that listed by Cooper (1934 : 8) and that only one specimen has so far been discovered in English rocks. However, A. J. Rundle (personal communication) after examining its matrix reports that it is a silicified specimen from the *Corbula* bed in the cliff at Reculver and not from the *morrisi* bed, as listed by Cooper.

Desorinassa williamsi sp. nov.

(Pl. 5, figs 1–3)

HOLOTYPE. Palaeocene, Ypresian, Bognor Rock, foreshore at Bognor, Sussex, GG 19706 (*B. A. Williams Colln.*).

PARATYPES. Some horizon and locality, GG 19707, (*Rev. A. Fuller Colln.*), and two internal moulds GG 19708/1–2 (*history unrecorded*).

FURTHER MATERIAL AND RECORDS. Unknown.

DIAGNOSIS. Large, stout, almost smooth *Desorinassa*; mean spire angle of about 60°; subsutural platform lacking; whorl profile convex; interior of outer lip not denticulate.

DESCRIPTION. The protoconch is unknown. Four whorls of the teleoconch survive; at least one or two earlier whorls are missing in all specimens. The whorls, which are broadest at the abapical suture, are convex except where recurved at the adapical margin to form an adpressed or almost flush suture. Spiral sculptural elements are lacking except for between six and eight weak ridges on the neck of the body whorl. Irregularly spaced collabral growth rugae of varying strength are developed. These, though weak, are distinctly stronger than growth lines. No ribs are present on the inner surface of the outer lip. Both internal moulds have a collabral groove about a quarter whorl before the aperture.

DIMENSIONS.	1	2	3	7	10	11
GG 19706 HT	27·8+	17·3	17·0	8+	—	—
estimated	29	—	—	—	1·68	1·71
GG 19707 PT	27·2+	17·2	17·9	5+	—	—
estimated	30	—	—	—	1·74	1·67
(see p. 192 for key)						

REMARKS. This species may be easily distinguished from *D. desori* which is smaller, and has a broad, sloping, subsutural platform with spiral ribbing on and near it. Two Cuisian species from the Paris Basin, *D. ovata* (Deshayes) (pl. 5, fig. 5) and *D. acies* (Watelet) (pl. 5, fig. 6) are much smaller than *D. williamsi* and possess fine spiral ribbing. The former is of a similar shape to *D. williamsi* but the latter is distinctly narrower.

WHITECLIFFIA gen. nov.

(Pl. 5, figs 6–12; Pl. 6)

TYPE SPECIES. *Buccinum suturosum* Nyst, 1836.

DIAGNOSIS. Differs from *Pseudocominella* only in the following respects: height less than 20 mm; protoconch of one and half whorls, initially deviated and bulbous; suture either weakly canaliculate or with narrow, flat, subsutural platform; no shoulder developed; collabral sculpture either absent or of weak grooves or ribs; columellar and parietal callus distinctly raised above general level of shell surface; fasciole similar to that of *Pseudocominella* but ridges and growth lines less prominent; outer lip seldom ribbed within.

OTHER SPECIES ASSIGNED. *Whitecliffia tumida* sp. nov.

GEOLOGICAL RANGE. Upper Eocene (Late Priabonian) to Middle Oligocene (Rupelian).

REMARKS. This genus seems likely to be an offshoot of *Pseudocominella.* It may readily be distinguished by its protoconch and by the relative smoothness of the teleoconch.

Whitecliffia suturosa (Nyst, 1836)

(Pl. 5, figs 6–11; Pl. 6, figs 1–4)

1836 *Buccinum suturosum* Nyst: 36, pl. 3, fig. 96.
1843 *Buccinum suturosum* Nyst; Nyst: pl. 43, fig. 16.
1845 *Buccinum suturosum* Nyst; Nyst: 579.
1867 *Buccinum suturosum* Nyst; von Koenen: 83, pl. 6 (1), fig. 3a, b, c.
1880 *Cominella* (*Buccinum*) *ventricosa* Edwards MS; Judd: 154.
1880 *Strepsidura suturosa* (Nyst) Bosquet: 467.
1881 *Cominella* (*Buccinum*) *ventricosa* Edwards MS; Keeping & Tawney: 116.
1886 *Strepsidura suturosa* (Bosquet); Vincent: 7.
1889 *Buccinum* (*Cominella*) *suturosum* Nyst; von Koenen: 242, pl. 21, figs 10a, b, c, 11a, b.
1901 *Cominella suturosum* (Nyst); Cossmann: 150.

1943 *Northia (Cominella) suturosa* (Nyst) Albrecht & Valk: 62, pl. 5, figs 140, 141.
1954 *Northia (Cominella) suturosa* (Nyst); Glibert & de Heinzelin: 367, 382, 392, 393, pl. 7, figs 4a, b.
1954 *Babylonia (Peridipsaccus) archambaulti* Meunier; Glibert & de Heinzelin: 368, 382, pl. 7, fig. 6.
1963 *Cominella suturosa* (Nyst); Glibert: 68.

LECTOTYPE. Middle Oligocene, Lower Rupelian, *Callista kickxi* horizon; *IRScNB* IG 3862, Klein Spauwen, Belgium (selected Glibert, 1963 : 68, figured Glibert, & de Heinzelin 1954, pl. 7, fig. 4b).

PARALECTOTYPE. Same details, *IRScNB* IG 3863, (figured Glibert & de Heinzelin, 1954, pl. 7, fig. 4a).

MATERIAL STUDIED. ENGLAND, Upper Eocene, late Priabonian, Middle Headon Beds, Royden, GG 19717 (*Ed*). Brockenhurst Bed, Whitecliff Bay, I.O.W., GG 19718 (*Wr*); (*Cu*). GERMANY, Lower Oligocene, Lattorfian, Latdorf, GG 19719/1–2 (*Ed*); GG 19720/1–2 (history unknown). BELGIUM, Lower Oligocene, Lattorfian (= Lower Tongrian), Grimmertingen *IRScNB* sample IG 5002 (*de Looz*). Middle Oligocene, Lower Rupelian, Klein Spauwen, GG 19721 (*de Koninck*). Berg, *IRScNB* sample IG 4285 (*Bosquet*).

FURTHER OCCURRENCES. HOLLAND, Lower and Middle Oligocene, South Limburg, in mine shafts (Albrecht & Valk, 1943 : 62). GERMANY, Middle Oligocene, Rupelian, Stettin Sands, Magdeburg, (von Koenen, 1889 : 242).

DIAGNOSIS. *Whitecliffia* with canaliculate suture; mean spire angle between 43° and 80°; whorls evenly convex with no shoulder developed; sculpture absent except for occasional weak spiral grooving; outer lip denticulate within.

DESCRIPTION. All the Belgian specimens and Wrigley's specimen from Whitecliff Bay are too badly worn to show sculptural details. The description is based mainly on the shells from Royden (GG 19717), Latdorf (GG 19719–20) and a specimen from Whitecliff Bay (*Cu*).

The mean spire angles of the lectotype, paralectotype and GG 19721 from Klein Spauwen are all under 50°. The spires of several specimens from Berg are also more acute than average. The English, Grimmertingen and Latdorf specimens are normally more tumid with the spire angle between 50° and 55°. The appearance of the suture is so considerably changed by wear, that this feature cannot be reliably used as a taxonomic feature. The better-preserved English and German specimens as well as most of the Belgian specimens have a narrow canaliculate suture and no subsutural ramp. Many of the Grimmertingen specimens, however, seem to have a fairly broad ramp and a less incised suture. In most specimens the sutures are not channelled for the first three or four whorls.

Below the suture the whorl profile is rather gently convex, and its periphery coincides with the abapical suture in most specimens. In shells with relatively acute spires, however, whorls are enveloped well below the periphery. About half the specimens have a relatively strong pad of callus in the parietal and columellar region which stands out above the rest of the shell-surface. The fasciole is not very rugose but the ridges on either side are fairly sharp when unworn. Only one specimen, the largest in sample *IRScNB* IG 5002 from Grimmertingen, has ribbing on the inner surface of its outer lip; this feature is also shown in one of von Koenen's figures (1889, pl. 21, fig. 10b). All the spire whorls of GG 19717 bear weak spiral grooves; eight may be counted on the penultimate whorl, but they become obsolete on the body whorl, which is smooth except for ten ribs on the neck. On another larger specimen (*Cu*), spiral grooves which are too poorly preserved to count, are present on the fourth and fifth whorls whilst the last two are smooth. GG 19719/1 and GG 19720/1, from Latdorf, however, have twelve grooves on the penultimate whorl, twenty-four on the body whorl and thirteen ribs on the neck below. Another specimen from Latdorf GG 19719/2 whose surface is also well preserved shows traces of spiral sculpture only on the neck.

Grimmertingen specimens are remarkable in having two or three relatively strong grooves just below the subsutural platform; below this weaker grooves may sometimes be distinguished. All other Belgian specimens seen from Berg and Klein Spauwen lack this grooving. No specimens show any trace of collabral sculpture other than growth lines.

DIMENSIONS.		1	2	3	10	11
GG 19717	actual	14·5	8·3	8·6	—	—
	estimated	15·5	—	—	1·87	1·80
GG 19720/1		16·1	9·1	9·1	1·77	1·77
GG 19720/2		16·9	10·0	8·9	1·69	1·90
GG 19721	actual	16·8	9·2	8·6	—	—
	estimated	17·5	—	—	1·90	2·03
GG 19719/2		18·8	10·1	9·0	1·88	2·09

(see p. 192 for key)

REMARKS. GG 19717 from Royden was labelled as *Cominella ventricosa* Edwards MS by Edwards; Keeping & Tawney's (1881 : 116) record is of this specimen. Judd's list (1880 : 154) was also compiled from the Edwards Collection, so his record of *C. ventricosa* from Colwell Bay, not Royden, is almost certainly a clerical error. Von Koenen (1867 : 83; 1889 : 242) quotes Royden as a locality. It therefore seems quite likely that he also examined this specimen, recognizing it to belong to *W. suturosa*. Grimmertingen specimens seem to represent a fairly marked variety, distinguished by the strength of the spiral grooving and by the usually less acute spire. A damaged specimen, *IRScNB* figd. spec. no. 4070 I.S.T. from Grimmertingen (pl. 5, figs 8a, b) identified as *Babylonia* (*Peridipsaccus*) *archambaulti* (Meunier) by Glibert & de Heinzelin (1954 : 368, 382, pl. 7, fig. 6) is definitely a *Whitecliffia* and may be an exceptionally large, broad example of the present species with a spiral angle of 80°.

Whitecliffia tumida sp. nov.

(Pl. 6, figs 5–10)

HOLOTYPE. Upper Eocene, Late Priabonian, Middle Headon Beds (*Venus* Bed), Whitecliff Bay, I.O.W. GG 19722/1 (*Cu*).

Paratypes. Same locality and horizon, GG 19722/2–7 (*Cu*); GG 19724 (*Cu*); GG 19723/1–3 (*Wr*); *Sedg. Mus.* C 29305 (*K&T*); (*Cu*); (*S*); GG 19756/1–3 (*S*) from Bed O of Stinton (1971 : 405).

Further occurrences. Unknown.

Diagnosis. Broad *Whitecliffia* with teleoconch of four or five whorls; mean spire angle of about 65°; whorl profile strongly convex; last whorl often rather swollen; collabral sculpture normally of up to sixteen strong, rather angular, costae which becomes less frequent and either die out or are replaced by broad flexures on pre-penultimate or penultimate whorl; spirally multistriate; subsutural collar obsolete; suture becoming slightly canaliculate on last whorl or so; outer lip rarely internally ribbed.

Description. None of the specimens examined is complete, and the form of the aperture is seen clearly only in one paratype. Whorls are enveloped just below the periphery. The whorl profile is more strongly convex in the early whorls before the collabral ribbing dies away. The whorl profile is almost horizontal at the adapical suture, and usually becomes grooved by the third or fourth whorl. The subsutural platform reaches a maximum width of 0·5 mm but seldom exceeds 0·3 mm wide; it is not separated from the rest of the whorl-side by a rib. The teleoconch starts with numerous weak, slightly opisthocline, collabral ribs. In the next quarter whorl these increase in strength and gradually adopt the orthocline attitude of the collabral ribs of the later teleoconch. There are normally about sixteen rather prominent, angular, collabral ribs on the first whorls of the teleoconch. They are weakest just below the suture and are of maximum strength from the shoulder to the adapical suture. On the third teleoconch whorl they weaken considerably; they may be just discerned on the fourth as faint flexures, which, on the body whorl, can be seen to die away below the periphery. GG 19724 is unusual. On the second whorl of its teleoconch about ten slight collabral crenulations occur for nearly half a whorl. This is strongly reminiscent of the start of collabral ribbing in other specimens, but dies away instead of developing further. On this specimen no other collabral sculptural elements exist except for growth lines. In the other specimens the spiral sculpture is first noticed within half a whorl of the collabral sculpture appearing. It consists of between six and ten irregularly spaced bands. Usually they can be seen to be ribs separated by interspaces wider than themselves. Often, however, and particularly on the last whorl, this separation is reduced and the shell becomes spirally multi-grooved. Bands of secondary strength may sometimes be seen. Spiral sculpture is either weak or absent from the periphery of the body whorl. Between seven and ten fairly prominent cords are present on the neck region. Internal ribbing of the outer lip is seen clearly only on one specimen (*Cu*) which has fifteen ribs extending back from the aperture for at least 45°. Irregular collabral colour bands up to about 1 mm broad separated by gaps of similar size may be seen on the last whorl of GG 19722/3 and one specimen (*Cu*); neither of these specimens shows spiral colour banding. GG 19722/6, however, shows spiral but not collabral colour banding. There is a dark band about 0·5 mm wide on the subsutural platform with a slightly narrower band just below the platform, below this there are indications of two more narrower bands well above the periphery.

DIMENSIONS.	1	2	3	8	10	11
GG 19722/1 HT	12·9	8·0	7·7	9+	1·61	1·67
GG 19722/2 PT	5·0	3·2	3·1	6+	1·56	1·61
GG 19722/4 PT	6·7	4·0	3·9	8+	1·67	1·72
GG 19722/5 PT	7·5	4·7	4·0	9+	1·60	1·88
GG 19722/7 PT	10·2	6·4	6·9	9+	1·59	1·73
(see p. 192 for key)						

REMARKS. This species closely resembles *W. suturosa* in shape and size. In the latter, collabral sculpture is almost non-existent, spiral sculpture though similar is weaker, and grooving of the suture occurs earlier and is more noticeable. As indicated, GG 19724 has unusual sculpture. It seems advisable, however, not to describe a separate species on the basis of a single specimen.

COLWELLIA gen. nov.

(Pl. 7)

TYPE SPECIES. *Cominella flexuosa* Edwards *in* Lowry, Etheridge and Edwards, 1866.

DIAGNOSIS. Agrees with *Pseudocominella* except in the following respects: seldom exceeds 20 mm height; protoconch of about two and a half smooth whorls, small, about 1 mm high, initially slightly flattened, first whorl very small; teleoconch sculpture developing gradually with collabral sculpture developing first; teleoconch with spiral and collabral sculpture of varying strength; subsutural platform either poorly developed or absent; growth lines of fasciole broadly sinuous as in *Desorinassa*; outer lip often denticulate within.

OTHER SPECIES ASSIGNED. *Nassa antiquata* Gabb, 1864 (pl. 7, fig. 11) *Buccinum auversiense* Deshayes, 1865 (pl. 7, figs 6, 7); *Ancillaria bretzi*, Weaver, 1912 (pl. 7, figs 8, 9); **Nassa cretacea*, Gabb, 1864; **Molopophorus tejonensis* Dickerson, 1915). (See p. 201 for explanation).

GEOLOGICAL RANGE. Middle Eocene (Auversian) to Upper Eocene (late Priabonian), Europe. Middle Eocene (Domengine Formation, California and Umpqua Formation, Oregon) to Upper Eocene (Cowlitz Formation, Washington and Tejon Formation, California), U.S.A.

REMARKS. The growth lines of the species assigned above to *Colwellia* are of the type found in *Pseudocominella* and all the other new genera described herein: they are approximately orthocline but are bent in an adoral direction in the sutural (adapical) region. In the lectotype (pl. 8, fig. 1a, b) of the type species of *Molopophorus*, *Bullia* (*M.*) *striata* Gabb, 1869 (*ANSP* 4249), the growth lines are bent away from the aperture in the sutural region, which appears to be canaliculate, as in *Brachysphingus* (pl. 8, figs 3, 4). The same feature is shown by *U.Cal.* 7182–30750 (pl. 8, fig. 2). However, another specimen figured as *Molopophorus striatus* by Dickerson (1915 : 67, pl. 8, fig. 6, given as fig. 7 in explanation to the plate) seems to be misidentified and is almost certainly a *Colwellia* (pl. 7, fig. 10).

The type of growth line found in *Molopophorus* (s.s.) and *Brachysphingus* is also found in *Cyllene*, a rare living genus of Nassariidae. This feature is found in other widely-separated prosobranch superfamilies and is often associated with a gutter or canaliculate suture which accommodates a posterior filament as in *Oliva* (Volutacea) (Tryon, 1883, pl. 3) and *Terebellum* (Strombacea) (Jung & Abbott, 1967, p. 446, pl. 319).

Sections through the columella of *Brachysphingus* show that it lacks the terminal plait found in all definite Nassariidae including *Cyllene*. Although no specimens of *Molopophorus* s.s. were available for sectioning (the lectotype is the only specimen in the ANSP collections—Dr H. G. Richards, personal communication), the external similarities of the two genera are so great that it is doubtful if either belongs to the Nassariidae. Their general shell features including the fasciole ridge and reverse S-shaped growth lines suggest that they may best be placed in the very broad Buccinidae (*sensu* Wenz, 1941–1943).

In fact, it seems that *Molopophorus* (Gabb, 1869 : 156) is a synonym—based on immature material—of *Brachysphingus* (Gabb, 1869 : 155), which is here selected as generic name of the taxon.

A large number of North American west coast Tertiary species ranging in age from the Meganos Formation (lower Eocene) of California (Clark & Woodford, 1927 : 117) to the Miocene of Washington State (Weaver, 1942 : 463–471) have been assigned to *Molopophorus* and the genus is also recorded from the Oligocene and Miocene of Japan (Oyama, 1960 : 73–74). These species differ considerably in form. Vokes, moreover, (1939 : 140–141) mentions that there were two or three distinct types of nuclear whorls among the Californian species ascribed to *Molopophorus* and suggested that they were unlikely to be congeneric. Most of these species need assigning to new genera—a task beyond the scope of this work. It would appear, however, that they are fairly closely related to the European forms described herein and would also seem to belong to the Nassariidae.

Gabb (1864 : 97) described *Nassa cretacea* and *Nassa antiquata* both of which have been regularly assigned to *Molopophorus* by American workers in this century. Nevertheless, he himself still assigned them to *Nassa* (1869, 219) in the paper in which he described *Molopophorus*. The difficulties of interpreting *Molopophorus* correctly have hindered workers who have suspected a connection between it and European species previously assigned to *Cominella*.

We have assigned to *Colwellia* only those American species which have a very strong resemblance to *C. flexuosa* and *C. auversiensis*.

In *Desorinassa* the ramp is convex and the collabral sculpture weak. In *Colwellia* the ramp is concave and the collabral sculpture is much stronger on the earlier whorls. *D. williamsi* (Ypresian) and *C. auversiensis* (Auversian) appear to form a link between the two genera.

The differences in the protoconch, given in the diagnosis, are sufficient to distinguish *Colwellia* from *Keepingia*, which almost certainly arose from it.

Colwellia flexuosa (Edwards, 1866)

(Pl. 7, fig. 1–5)

1866 *Cominella flexuosa* Edwards *in* Lowry, Etheridge & Edwards, pl. 3.
1880 *Cominella* (*Buccinum*) *flexuosa* Edwards MS; Judd: 154.
1881 *Cominella* (*Buccinum*) *flexuosa* Edwards MS; Keeping & Tawney: 105, 116.
1889 *Cominella flexuosa* Lowry; Bristow: 290.
1891 *Cominella flexuosa* Edwards MS; Newton: 168.
1921 *Cominella flexuosa* Edwards; Wrigley: 139.
1926 *Cominella flexuosa* Edwards; Jackson: 356.
1963 *Cominella flexuosa* Edwards *in* Lowry; Glibert: 67.

LECTOTYPE (designated herein). Upper Eocene, late Priabonian, Middle Headon Beds (presumably *Venus* Bed), Colwell Bay, I.O.W., GG 19709/1 (*Ed*).

PARALECTOTYPES (designated herein). Same details, GG 19709/2–30.

MATERIAL STUDIED. Restricted to Middle Headon Beds. *Venus* Bed, Colwell Bay, GG 19710/1–11 (*Wr*); GG 19711 (*Nu*); (*Cu*); (*S*); *Sand. Mus.* 4778, 748; *Sedg. Mus.* C 28281–4 (*K&T*). Headon Hill, I.O.W., GG 19712/1–3 (*StJB*); *Sedg. Mus.* C 28645–9 (*K&T*). *Venus* Bed, Whitecliff Bay, I.O.W., GG 19713 (*Cu*). Brockenhurst Bed, Brockenhurst, GG 19714 (*Ed*).

FURTHER OCCURRENCES. Unknown.

DIAGNOSIS. *Colwellia* with narrow sloping subsutural collar and rather broad concave subsutural ramp; mean spire angle between 55° and 70°; angular cancellate ribbing on early whorls, becoming almost smooth, particularly below periphery of last whorl; outer lip often weakly denticulate within; obvious sinus in growth lines of peripheral region, and in some specimens a posterior siphonal notch, developed at maturity.

DESCRIPTION. The protoconch is worn in all specimens, the junction with the teleoconch cannot be seen. The aperture is slightly more than two-thirds shell height. The teleoconch consists of up to five whorls. The suture normally lies on the periphery, sometimes on later whorls it lies just below as the sutural slope increases slightly. Below the rounded subsutural band the very slightly concave ramp slopes away to the shoulder. Three or four weak spiral ribs occur on and below the shoulder of spire whorls; that on the shoulder is the strongest. These ribs become noticeably weaker on the last whorl. Up to two more spiral ribs, which are usually weaker, may occur on the ramp. Between five and ten rather widely spaced spiral cords are present on the neck of the body whorl. The collabral ribs are stronger than the spiral ones and are like crested-waves in cross-section. There are about twenty-one collabral ribs on the spire whorls of the teleoconch. On the first half of the body whorl there are about sixteen increasingly weaker ribs. Collabral ribbing becomes virtually obsolete on the final half whorl. The main indication of its presence is slight axial nodes on the spiral ribs. Similar nodes are formed on the spire whorls where the collabral and spiral ribs intersect giving a rather cancellate appearance. In some specimens the outer lip is smooth internally, in others there are up to fifteen unevenly spaced weak denticles about 1 mm long and set about 1 mm inside the aperture, and a few shells show another row of denticles about 45° inside the aperture. As well as the broad sinus in the growth lines of the peripheral region of mature specimens there is a slight posterior siphonal notch developed in the outer lip where it meets the suture (pl. 7, fig. 2c). Its strength seems related to the size of the shell and it is sometimes absent in smaller specimens. It may be presumed to mark the reaching of full growth as there is no trace, except occasionally on the last quarter whorl, of its previous existence on earlier growth lines. In a few specimens the colour pattern is clearly visible under ultra-violet light. A pair of spiral bands, about 0·5 mm wide, separated by about 0·2 mm lie on the periphery (thus appearing just above the suture on spire whorls). Another pair of bands, about half the breadth, occurs at the top of the neck.

DIMENSIONS.	1	2	3	4	5	6	7	8	9	10	11
GG 19709/1 LT	14·2	9·5	9·0	5	14	22	14	6	5	1·49	1·58
GG 19713 —	5·4	3·3	3·2	3	17	20	5+	4	0	1·63	1·68
GG 19709/6 PLT	10·8	6·8	6·6	4½	22	22	12+	4	0	1·59	1·64
GG 19709/2 PLT	14·3	8·3	8·6	5	22	21	12+	7	6	1·72	1·66
GG 19709/4 PLT	14·9	9·4	9·2	5	18	23	15+	7	0	1·58	1·62
GG 19709/3 PLT	20·1	13·0	11·2	6	9	25	28	10	15	1·55	1·79

(see p. 192 for key)

REMARKS. Following Wrigley's (1921 : 139) reasoning, we ascribe the authorship of this species to F. E. Edwards. Its resemblance to the earlier *C. auversiensis* (Deshayes) (pl. 7, figs 6, 7) is striking. Both species have teleoconchs so similar to those of *Keepingia* that it is necessary to compare them with both *K. gossardi* (Nyst) (pl. 8, figs 5–7) and *K. cassidaria* (Sandberger) (pl. 8, fig. 9). *C. auversiensis* differs from both *C. flexuosa* and *K. cassidaria* in being less tumid, having a less concave ramp and less marked shoulder whilst its collabral sculpture, though weaker on early growth stages is more persistent and its growth lines less flexuous. Sandberger figures two varieties of *K. cassidaria*. The first (1863, pl. 20, figs 1, 1a, 1d, 1e) is characterized by about four strong spiral ribs on the spire whorls and about ten on the body whorl. It lacks collabral sculpture on the last and sometimes on the penultimate whorl. The second variety (1863, pl. 20, figs 1b, 1c) which he refers to (p. 230) as var. *cancellata*, is less common in B.M.(N.H.) collections. It has a cancellate appearance; the primary spiral ribs are separated by secondary ones and numerous collabral rugae are developed. Both forms of *K. cassidaria* may be readily distinguished from *C. flexuosa* by their sculpture. *K. gossardi* differs from *C. flexuosa* by being larger and having a relatively smaller aperture, less sinuous growth lines, and more definite subsutural collar with a tendency for the suture to be canaliculate. The sculpture of *K. gossardi* is much stronger and persists to maturity. It has numerous spiral ribs and about fifteen collabral folds per whorl.

Two specimens in the F. E. Edwards Collection (GG 19725–6) were labelled by Edwards as being from the Bracklesham Beds of Brook, Hampshire. The first was correctly identified as *flexuosa* and appears from the matrix to be from the Brockenhurst Bed of the Brockenhurst area. The second is likely to be from Brook but is a young *Strepsidura turgida* (Solander). The sculpture on the spire whorls of these two species is remarkably similar. Edwards' label may have caused Keeping & Tawney (1881 : 105, 116) to indicate that the species occurs in strata older than the Headon Beds.

There is a remarkably small variation in size of the known specimens. Most of those in B.M.(N.H.) collections lie between 12 and 16 mm in height. The largest and smallest specimens whose dimensions are given here are exceptional.

KEEPINGIA gen. nov.

(Pl. 8, figs 5–9)

TYPE SPECIES. *Buccinum gossardi* Nyst, 1836.

DIAGNOSIS. Agrees with *Colwellia*, except in the following respects; sometimes exceeding 20 mm in height; protoconch initially slightly heterostrophic, of one and a half smooth whorls, separated from teleoconch by a whorl on which there are about 20 decreasingly opisthocline collabral folds, with spiral sculpture developing on later part.

OTHER SPECIES ASSIGNED. ***Cominella annandalei* Vredenburg 1925; ***Cominella aturensis* Peyrot, 1927; *Buccinum bolli* Beyrich, 1854; *Buccinum cassidaria* Sandberger, 1863; ***Cominella praecedens* Peyrot 1927; *Nassa tarbellica* Grateloup, 1834; ***Buccinum uniseriale* Sandberger, 1863. (See p. 201 for explanation.)

GEOLOGICAL RANGE. Lower Oligocene (Late Lattorfian) to Lower Miocene (Burdigalian).

REMARKS. The similarities of the teleoconch suggest that *Keepingia* is close to *Colwellia* but its consistently different protoconch in all species examined justifies its separation. It is the only genus described herein that survives into the Miocene. The first occurrence is of the type species in the Upper Tongrian Henis Clay of Belgium, the species persists into the Rupelian of Belgium and France. The last definite occurrence of the genus is that of *K. tarbellica* in the Burdigalian of the Bordeaux basin.

As indicated above no specimens of four of the species listed were available for study, so the stratigraphical and geographical range of the genus as shown on Table 1 can only be tentative. This is particularly unfortunate in the cases of *C. annandalei* from the Nari (Oligocene) of the Indian sub-continent. No species are known from England.

THANETINASSA gen. nov.

(Pl. 9, figs 1–7)

TYPE SPECIES. *Buccinum bicorona* Melleville, 1843.

DIAGNOSIS. *Phos*-like, relatively tall, up to about 20 mm high; teleoconch of up to six whorls; mean spire angle of about 45°; aperture about half shell height; strong, slightly sloping, subsutural platform developed; both spiral and collabral ribbing strong, with beads produced at intersections; outer lip notably convex, only slightly produced anteriorly; growth lines markedly recurved in neck region immediately prior to terminal aperture, to form a 'stromboid-like' notch, associated with particularly strong spiral ribbing; columella bent to the right above a terminal plait; growth lines of fasciole as in *Desorinassa;* columellar and parietal callus weakly developed.

OTHER SPECIES ASSIGNED. None.

GEOLOGICAL RANGE. Palaeocene (Thanetian).

REMARKS The strong 'stromboid-like' notch developed at the final aperture immediately distinguishes this genus from the others described in this paper. All these have a slight sinuosity in a similar position, but nothing so marked. In living *Strombus* the notch accommodates the right eye peduncle.

Both *Phos* and *Nassarius* s.l. have similar notches. It is always strong in *Phos*, but is of variable strength in *Nassarius*. The eye tentacles of *Phos* are joined at their base to form a Y-shaped structure (Tryon, 1881 : 215, pl. 83, fig. 484), in *Nassarius* (Tryon, 1882, pls 7, 9, 12, 14, 15, 18) the arrangement is rather similar. It seems possible that this structure as a whole, rather than a single tentacle, lay underneath the notch.

It is hoped that the relationship between the Nassariidae and the *Phos*-like genera which were assigned to the Buccinidae by Wenz (1941) will be discussed in a future paper in greater detail than would be appropriate here. The curved columella, the form of the columellar plait, with its strong posterior boundary ridge and the broad fasciole of *Thanetinassa* are very similar to those of contemporary *Desorinassa*, which differs in having very weak sculpture The later genus *Pseudocominella* is strongly sculptured and *P. solanderi* is similar in shape and size to *T. bicorona*. Any similarity in their sculpture, however, is superficial. Moreover, the columellar and fasciole features of the two genera are very different.

Thanetinassa should be compared with *Buccitriton* and *Tritiaria* (both assigned by Wenz, 1941 : 1177–1178, to the Buccinidae) and *Sagenella* (tentatively assigned by Wenz, 1943 : 1224, to the Nassariidae) All three genera occur in the Lower Tertiary of the South-Eastern United States. In all three the fasciole is bounded posteriorly by a much weaker ridge than in *Thanetinassa*, and the stromboid notch is either weak or absent and is never associated with strong spiral ribs. In *Buccitriton* the columella is short, terminating well above the most anterior part of the shell, which in this case is the outer lip. In *Thanetinassa*, on the other hand, the terminal columellar plait forms the most anterior portion of the shell. In *Tritiaria* the fasciole is much narrower than in *Thanetinassa* and is spirally striate.

Thanetinassa bicorona (Melleville, 1843)

(Pl. 9, figs 1–7)

1843 *Buccinum bicorona* Melleville: 12, 73, pl. 10, figs 4, 5.
1850 *Buccinum bicorona* d'Orbigny: 303.
1865 *Buccinum quoesitum* Deshayes: 503.

1866 *Buccinum quoesitum* Deshayes: pl. 93, figs 9–12.
1889 *Cominella bicoronata* (Melleville) *nom. mut.* Cossmann: 138.
1901 *Cominella bicorona* (Melleville); Cossmann: 150.
1911 *Cominella bicoronata* (Melleville); Cossmann & Pissaro, pl. 37, fig. 178–7.
1934 *Cominella bicoronata* (Melleville); Cooper: 7.
1963 *Cominella bicorona* (Melleville); Glibert: 66.

MATERIAL STUDIED. ENGLAND, Palaeocene, Thanetian, Upper Thanet Sands' *Corbula* Bed. Herne Bay, Kent, G 57073–8 (*J. E. Cooper Colln.*). Bishopstone' Herne Bay, G 60746 (*J. E. Cooper Colln.*); GG 19741/1–2 (*Wr*); GG 19742 (*Wr*); GG 19743 (*A. G. Davis Colln.*). Bishopstone Gap, GG 19744 (*Ru*). *Arctica morrisi* Bed, foreshore exposure approx. 400 yards E. of Bishopstone Gap, GG 19745 (*Ru*). FRANCE, Palaeocene, Thanetian, Châlons-sur-Vesle, Marne, G 19357/1–4 (*L. Staadt Colln.*); GG 19740 (*Wr*); 5 shells *EMP* (*Deshayes Colln.*).

FURTHER OCCURRENCES. FRANCE, Sable Inférieurs (Thanetian). TYPE LOCALITY Villiers-Franqueux (Melleville, 1843 : 73). Châlons-sur-Vesle, Brimont, Jonchery (Deshayes, 1865 : 503; Châlons-sur-Vesle (Briart & Cornet, 1871 : 31); Châlons-sur-Vesle, Chenay, Jonchery (Glibert, 1963 : 66).

DIAGNOSIS. As for genus.

DESCRIPTION. All the specimens are fragile, abraded, and with their earlier whorls either missing or decorticated. It is impossible therefore to separate the protoconch and teleoconch. GG 19741/2, however, is 12·3 mm high and has eight whorls. Neither definite ribbing nor the subsutural platform appear until the fourth whorl, so the first three may well comprise a rather acutely-spired, naticoid, protoconch. Most of the spiral ribs are distinctly weaker than the collabral ones and the preservation in all specimens is such that spiral ribs cannot be seen until the third teleoconch whorl. Up to nine spirals ribs occur on the spire whorls and about twenty on the body whorl. The two strongest, which are stronger than any of the collabral ribs, are those forming the sloping subsutural platform and the shoulder. The concave ramp is formed in the interspace between these two ribs. Sometimes two or three other fairly strong ribs occur on the neck above the fasciole, marking a backwardly-directed fold in the growth lines. Sometimes a weak rib is developed above the main rib of the subsutural platform. The collabral ribs are more or less orthocline and decrease in strength below the periphery; on some specimens they may be seen to follow the above-mentioned fold on the neck. They are prominent, steep-sided, and separated by interspaces nearly twice their width. Their number remains fairly constant, throughout growth. On the last whorl, their spacing becomes less regular. An irregular, varix-like, pre-terminal aperture is often developed just after the commencement of the last whorl, being situated on the ventral surface of the shell, slightly to the left of the final aperture. Similar varices may well be developed later on the last whorl, GG 19744 having a total of five. Two weak spiral ribs are occasionally developed on the fasciole. Spiral ribbing has not been seen within the outer lip.

Dimensions.		1	2	3	4	5	6	7	8	9	10	11
GG 60746		18·5	—	—	—	—	—	19	—	—	—	—
	estimated	20·0	—	9·0	6	25	—	—	—	—	—	1·77
G 1974/1		17·5	—	8·0	—	—	—	19	9	—	—	—
	estimated	18·5	—	—	6	22	—	—	—	—	—	2·31
GG 19741/2		12·3	—	6·0	5–6	15	20	20	8	—	—	2·01
GG 19357/1		15·5	8·5	8·3	6	23	24	18	8	—	—	—
	estimated	16·0	—	—	—	—	—	—	—	—	1·88	1·93
GG 19357/2		14·6	7·0	8·3	6	19	19	21	8	—	2·08	1·76
GG 19357/3		12·8	6·0	6·3	6	23	21	16	7	—	1·70	1·61

Remarks. The English specimens are notably more strongly varicate on the last whorl than those from France. There are, however, no other apparent grounds for specific separation. This species strongly resembles *Buccinum montense* (pl. 9, figs 8a, b) described by Briart & Cornet (1871 : 30–31) from the Montian 'Calcaire Grossier' of Mons; they compare the two species in detail, and both were subsequently assigned to *Cominella* by Cossmann (1901 : 150). Examination of the fasciole of *Buccinum montense* from Mons (GG 71604–7, *Chavan Colln.*) show that this species is not a member of the Nassariidae but is congeneric with European Eocene and Oligocene species assigned to *Pollia* of the Buccinidae.

Cossmann (1889 : 138) placed *B. quoesitum* Deshayes (1865) in the synonomy of *B. bicorona* Melleville (1843) remarking that Deshayes had overlooked the earlier name. The whereabouts of Melleville's specimens is unknown but his figures (1843, pl. 10, figs 4, 5) appear to agree with those of Deshayes (1866, pl. 93 figs 9–12) and Deshayes' surviving specimens all from Châlons-sur-Vesle (*EMP*). Melleville's locality was Villers Franquex, at which the only horizon exposed is the middle fossiliferous zone of the Sables de Châlons-sur-Vesle (Fritel, 1910 : 332).

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PLATE 1

Pseudocominella deserta (Solander) p. 190

Upper Eocene, early Priabonian, Barton Beds, Barton-on-Sea, Hampshire.

FIGS 1–9

FIGS 1a, b. Lectotype, *Brander Colln.* GG 19667. ×2.

FIG. 1c. Same, oblique view to show subsutural platform. ×3.

FIG. 2. Paralectotype, *Brander Colln.* GG 19668. ×2.

FIG. 3. GG 19678/1 (*Wr*). Horizon H, Upper Barton Beds. ×4.

FIG. 4. GG 19676/1 (*StJB*). Middle Barton Beds, ×2·5, sectioned to show columellar plait.

FIG. 5. GG 19672/2 (*Le*), same sample as figs 8a, b, Horizon A3, Lower Barton Beds, oblique view to show development of sculpture. ×6.

FIG. 6. GG 19671 (*Ru*). Horizon A2, Lower Barton Beds, showing differences in sculpture compared with fig. 5. ×6.

FIGS 7a, b. GG 19675 (*Ru*). Horizon B, Lower Barton Beds, showing widening of interspaces between axial ribs on rear of last whorl. ×2·5.

FIG. 8a, b. GG 19672/1. Same sample as fig. 5, to show details of fasciole and columella. Fig. 8a ×6, fig. 8b ×9.

FIG. 9. GG 19670/5 (*Ed.*) Side view to show shape of outer lip, particularly the forward bend of growth lines at the suture and the slight notch or sinus near the anterior end of the mouth. ×2.

FIGS 10, 11. Upper Eocene, early Priabonian, Westeregeln, Germany, (*Ed*).

FIG. 10. GG 19680/2. ×3.

FIG. 11. GG 19680/1. Protoconch. ×22 (stereoscan).

FIG. 12. Upper Oligocene, late Priabonian, Brockenhurst Bed, Middle Headon Beds, Whitecliff Bay, Isle of Wight, specimen collected by and listed by Keeping & Tawney (1881 : 116), *Sedg. Mus.* C 29122. ×2.

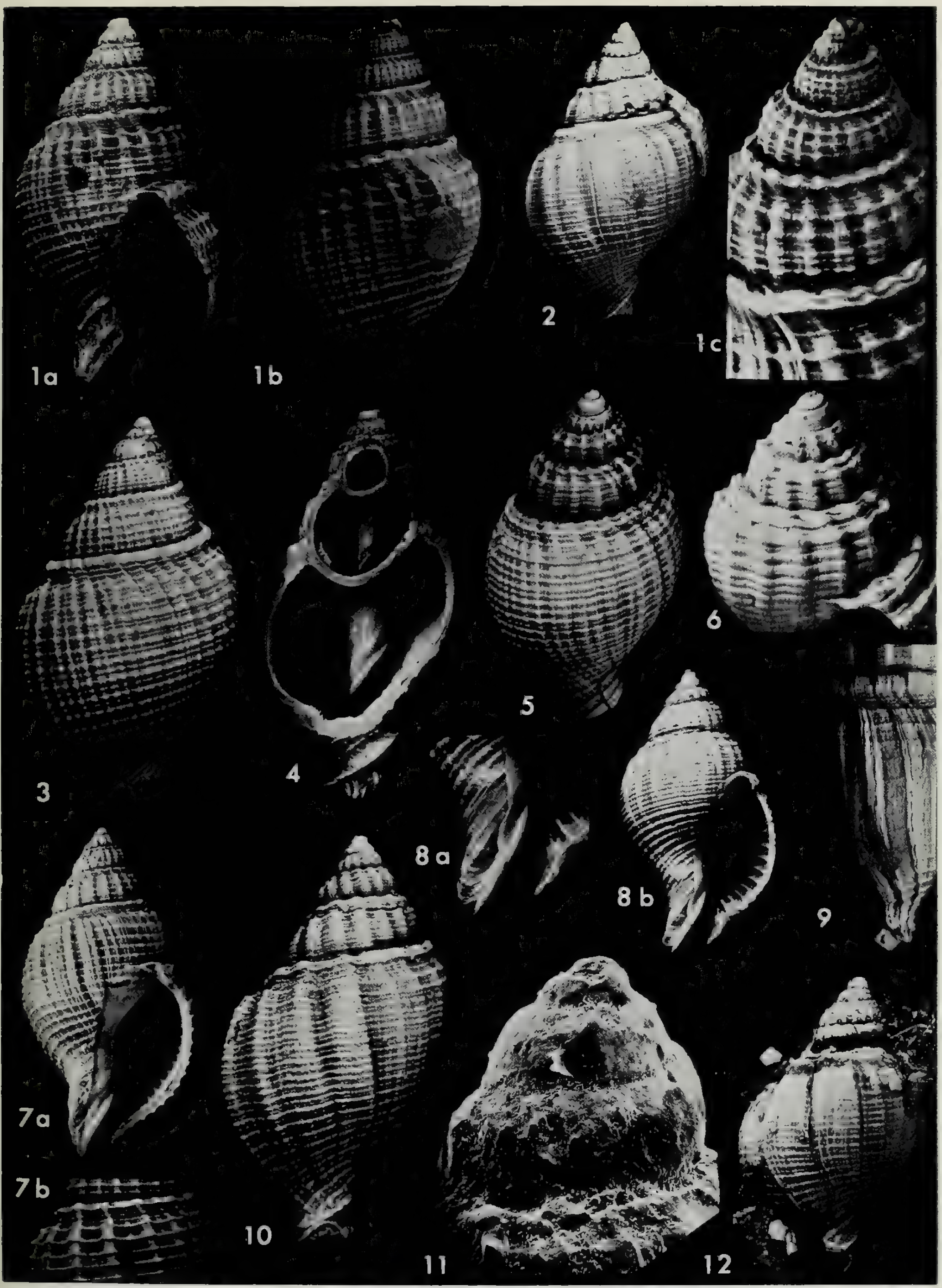

1a
1b
2
1c
3
4
5
6
8a
8b
9
7a
7b
10
11
12

PLATE 2

FIGS 1–8

Pseudocominella solanderi (Cossmann) p. 198

Upper Eocene, early Priabonian, Lower Barton Beds, Barton-on-Sea, Hampshire.

FIGS 1a–d. Neotype, GG 19693/1 (*Ho*). Horizon A3. ×4. Fig. 1d. Oblique view to show colour-bands separated by the spiral rib which marks the weak shoulder of the last whorl.

FIG. 2. GG 19694/1 (*Le*), same sample as figs 3, 6, 8, Horizon A3, relatively tumid specimen. ×3.

FIG. 3. GG 19694/2, same sample as figs 2, 6, 8 showing unusually persistent axial ribbing and colour-banding. ×5.

FIG. 4. GG 19698/1 (*Nu*). Horizon A2, juvenile shell showing early sculpture, and colour-banding on shoulder. ×6.

FIG. 5. GG 19695/2 (*S*). Horizon A3, same sample as fig. 7, juvenile. ×6.

FIG. 6. GG 19694/3, same sample as figs 2, 3, 8, adult shell with persistent strong axial ornament, and colour-banding. ×3.

FIG. 7. GG 19695/1, same sample as fig. 5, mouth of gerontic shell. ×4.

FIG. 8. GG 19694/4, same sample as figs 2, 3, 6, protoconch, the erect appearance of the first whorl is due to weathering. ×24 (stereoscan).

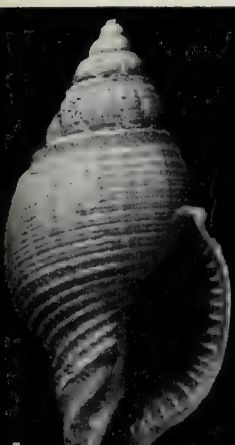
FIGS 9a, b

Pseudocominella bullata (Philippi) pp. 189, 193, 198

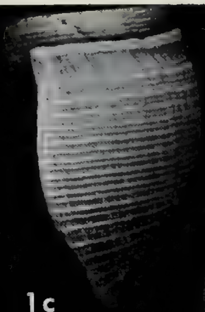
Lower Oligocene, Lattorfian, Latdorf, Germany, GG 19736/1 (*Ed*).

FIG. 9a. Showing lack of axial sculpture on early whorls. ×2.

FIG. 9b. Showing protoconch and development of spiral sculpture. ×12.



1a



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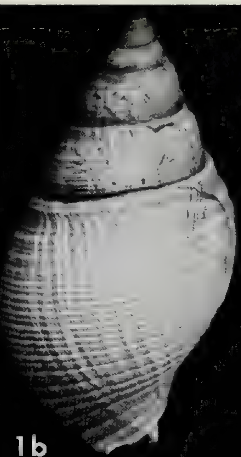

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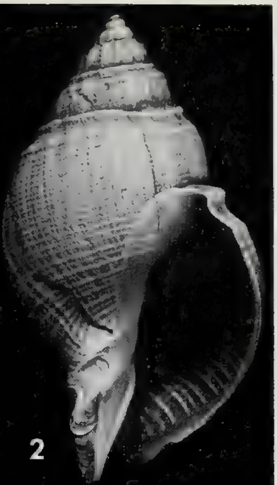

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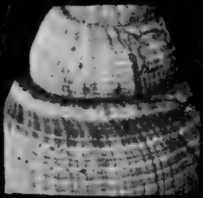
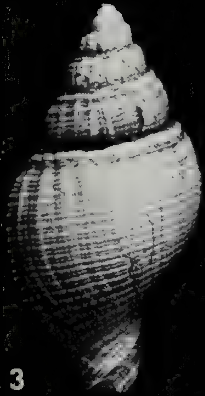


1d



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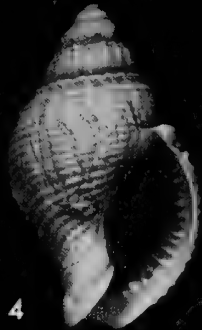

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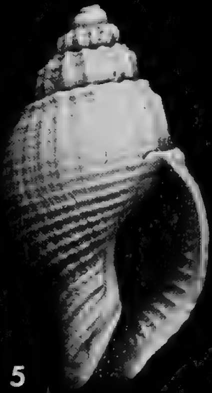

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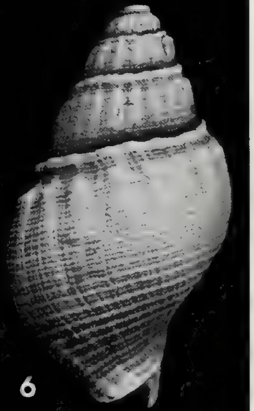

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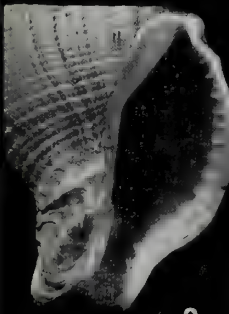

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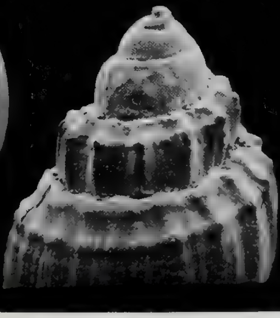

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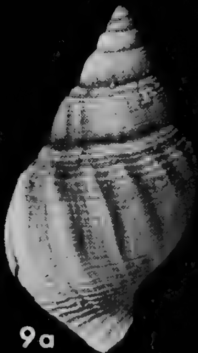

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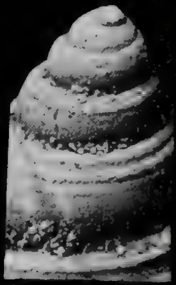

9b

PLATE 3

FIGS 1–6

Pseudocominella armata (J. de C. Sowerby) p. 193

Middle Eocene, Auversian, Upper Bracklesham Beds.

FIGS 1a, b. Neotype. GG 19681/1 (*Ed.*), Bracklesham Bay, Sussex. ×2.

FIGS 2–4. GG 19685/1–3 (*Ed*), Bramshaw, Hampshire.

FIG. 2a. GG 19685/3. ×2.

FIG. 2b. GG 19685/3. Showing fasciole. ×5.

FIG. 3. GG 19685/2. Oblique view showing development of strong sculpture and preterminal apertures on last whorl. ×3.

FIG. 4. GG 19685/1. Early whorls. ×12 (stereoscan).

FIG. 5. GG 19683/1 (*Ed*), Brook, Hampshire, oblique view showing relatively weak sculpture. ×3.

FIG. 6. GG 19684 (*Ed*), Huntingbridge, Hampshire. ×3·5.

FIGS 7, 8

Pseudocominella armata (J. de C. Sowerby)

Paris Basin, referred to by Deshayes 1865 : 499 as *Buccinum fusiforme* Deshayes, (*Deshayes Colln., EMP*).

FIG. 7. Specimen from either Le Fayel, Mary or Caumont, Auversian, oblique view showing sculpture. ×3.

FIG. 8. Specimen from either Vendrest, Auvers or Acy, all Auversian (see p. 194 for explanation). ×3.

FIGS 9–10

Pseudocominella semicostata sp. nov. p. 196

Upper Eocene, Late Priabonian, Middle Headon Beds, Royden, Hampshire (*Ed*).

Both specimens referred to as *Strepsidura armata* (J. de C. Sowerby) by all previous authors.

FIG. 9. GG 19686/5. Juvenile shell. ×5.

FIGS 10a, b. GG 19686/3. Larger shell showing gradual development of peripheral spines. ×3.

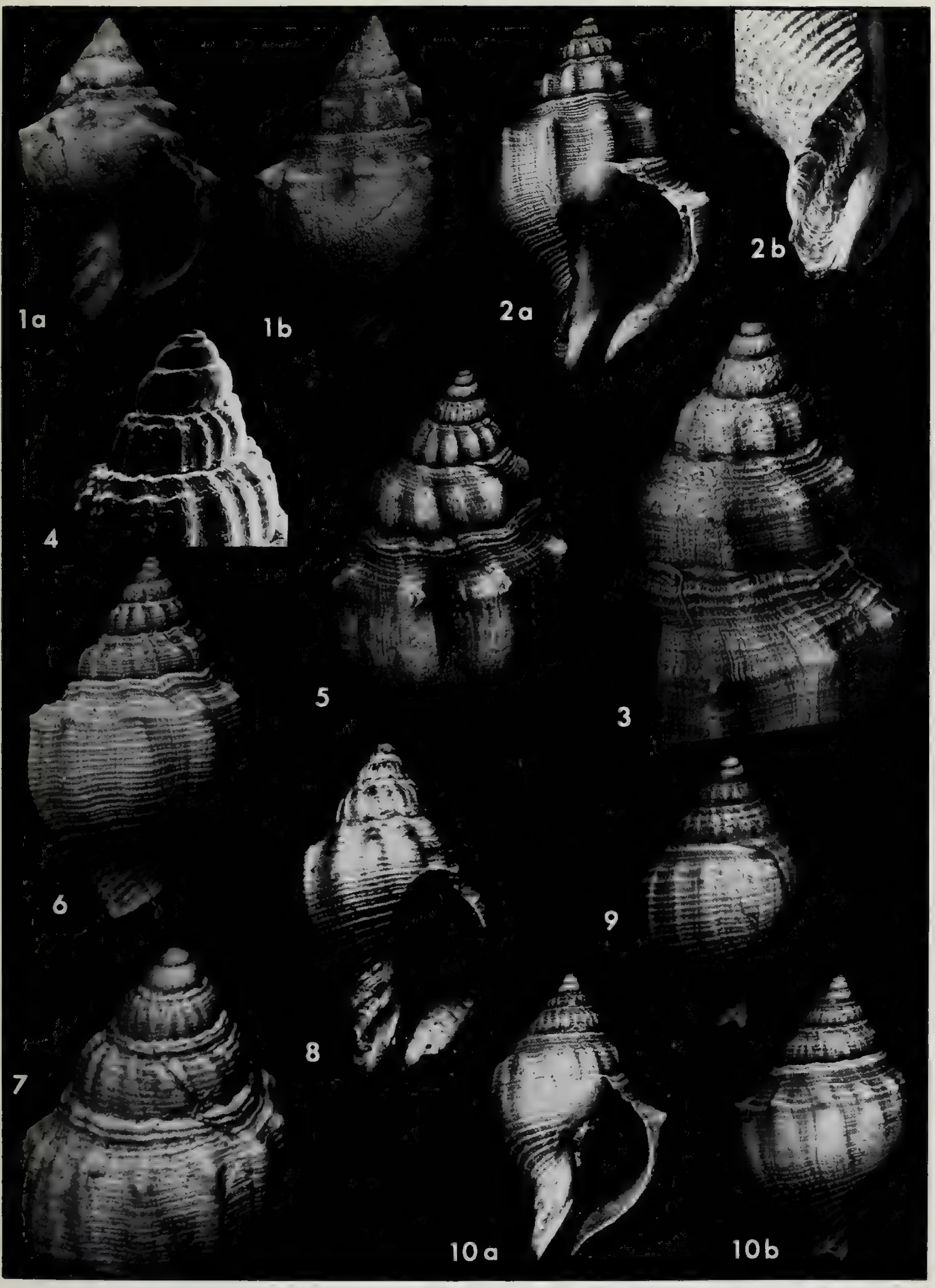
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PLATE 4

FIGS 1–3

Pseudocominella semicostata sp. nov. p. 196

Upper Eocene, late Priabonian, Middle Headon Beds.

All specimens referred to as *Strepsidura armata* (J. de C. Sowerby) by all previous authors.

FIGS 1–2. Whitley Ridge railway cutting, Brockenhurst, Hampshire (*Ed* ex *K*).
FIGS 1a, b. Holotype, GG 19687/1. ×2.
FIG. 2. Paratype, GG 19687/2. ×2·5.
FIG. 3. GG 19688/14, Brockenhurst, Hampshire, broken paratype showing columella. ×3.

FIGS 4–7

Desorinassa desori (Deshayes) p. 202

Palaeocene, Thanetian.

FIGS 4–6. Jonchery-sur-Vesle, France.

FIGS 4a, b. GG 19438/1 (*L. Staadt Colln*). ×3. Fig. 4b. Slightly oblique side view to show labial profile, posterior flaring of outer lip and subsutural platform.

FIG. 5. GG 19438/2 (*L. Staadt Colln*), oblique view of younger shell. ×4.

FIG. 6. GG 19705/1 (*Wr*). Oblique view of even younger shell with weaker spiral sculpture and showing naticoid protoconch comparable with that of *Pseudocominella*. ×4.

FIGS 7a, b. GG 19704, Thanet Sand, Reculver, Kent. (*Wr*), possibly the specimen referred to by Cooper (1934 : 8) (see remarks, p. 203). ×2.

FIGS 8, 9

Desorinassa lata (Deshayes) p. 201

Palaeocene, Thanetian, Abbecourt and Bracheux, France.
(*Deshayes Colln, EMP*) with no indication as to which specimen comes from which locality.

FIG. 8. Lectotype, selected herein.
FIG. 9. Paralectotype selected herein. Both ×1·67.

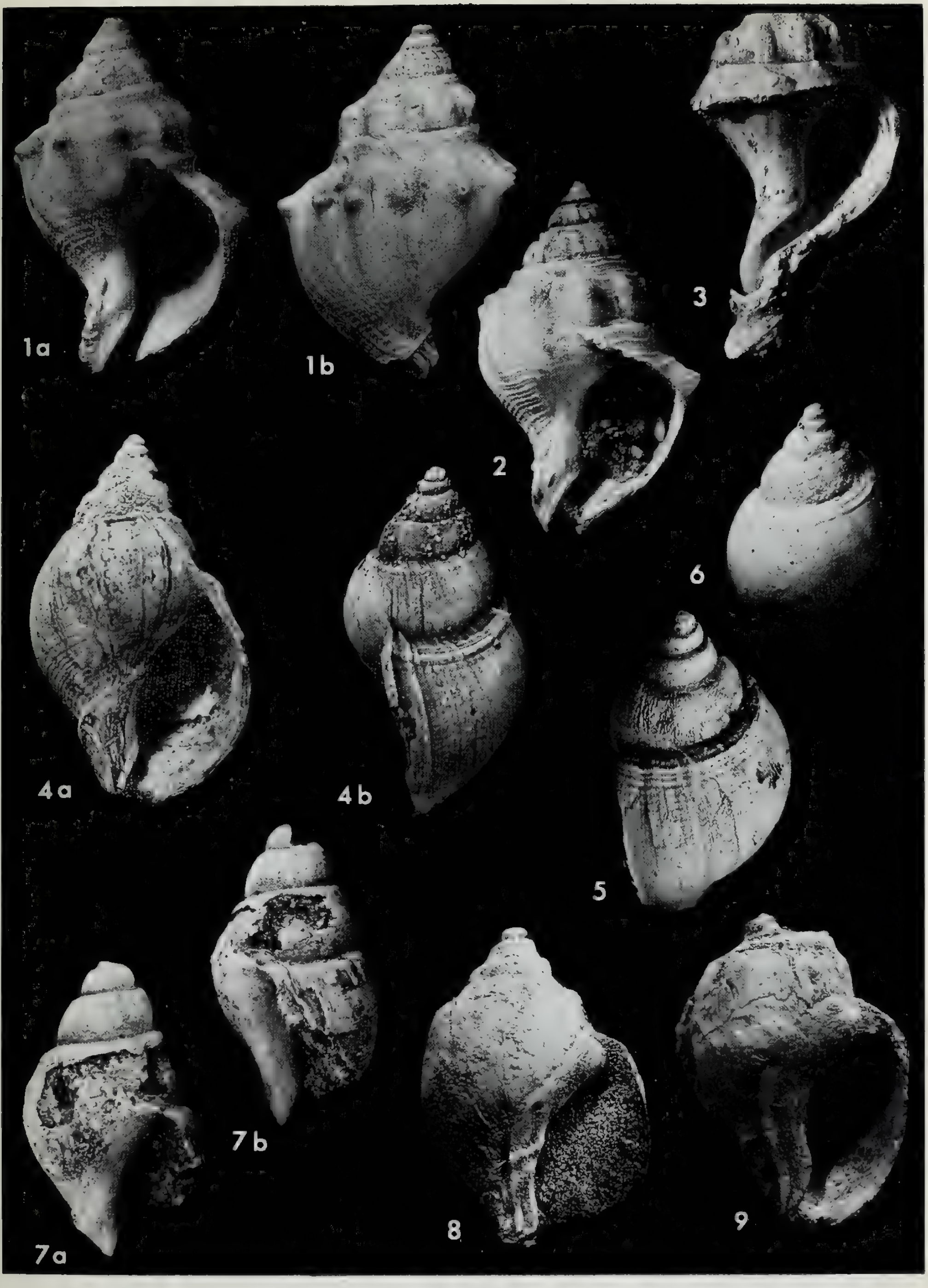
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PLATE 5

FIGS 1–3

Desorinassa williamsi sp. nov. p. 203

Palaeocene, Ypresian, Bognor Rock, foreshore at Bognor, Sussex.

FIGS 1a, b. Holotype. GG 19706 (*Williams Colln*). ×2.

FIG. 2. Paratype. GG 19707 (*Rev. A. Fuller Colln*). Oblique view showing details of fine sculpture on last whorl. ×4.

FIG. 3. Paratype. GG 19708/1, probably from Bognor, history unknown, internal mould. ×1·6.

FIG. 4

Desorinassa ovata (Deshayes) p. 201

Lower Eocene, Cuisian, Cuise, France.

(*Deshayes Colln, EMP*) probably referred to by Deshayes, 1866 : 497. ×4.

FIG. 5

Desorinassa acies (Watelet) p. 201

Lower Eocene, Cuisian, Sapicourt, France.

IScRNB sample IG 10591, fig. spec. no. 5600 I.S.T., referred to by Glibert (1963 : 66). ×3.

FIGS 6–11

Whitecliffia suturosa (Nyst) p. 204

Lower and Middle Oligocene, Belgium.

FIGS 6–8. (*de Looz Colln., IRScNB*) sample IG 5002, Lower Oligocene (Lattorfian = Lower Tongrian) Grimmertingen specimens referred to by Glibert & de Heinzelin (1954 : 382).

FIG. 6. Fig. spec. no. 5602 I.S.T., tumid specimen. ×2·7.

FIGS 7a, b. Fig. spec. no. 5603 I.S.T., typical specimen. Fig. 7a, ×2·7; Fig. 7b, oblique view to show protoconch and spiral sculpture on ramp. ×3·5.

FIGS 8a, b. (*IRScNB*). Fig. spec. no. 4070 I.S.T., Grimmertingen, specimen referred to as *Babylonia* (*Peridipsaccus*) *archambaulti* (Meunier) by Glibert & de Heinzelin (1954 : 368, 382, pl. 7, fig. 6). ×2.

FIGS 9–11. Middle Oligocene, Lower Rupelian.

FIG. 9. GG 19721. (*de Koninck Colln*), Klein Spauwen. ×3.

FIGS 10, 11. (*Bosquet Colln., IRScNB*) sample IG 4285, Berg. Specimens referred to by Glibert & de Heinzelin (1954 : 392, 393).

FIG. 10. Fig. spec. no. 5604 I.S.T. ×2·5.

FIG. 11. Fig. spec. no. 5605 I.S.T. ×2·5.

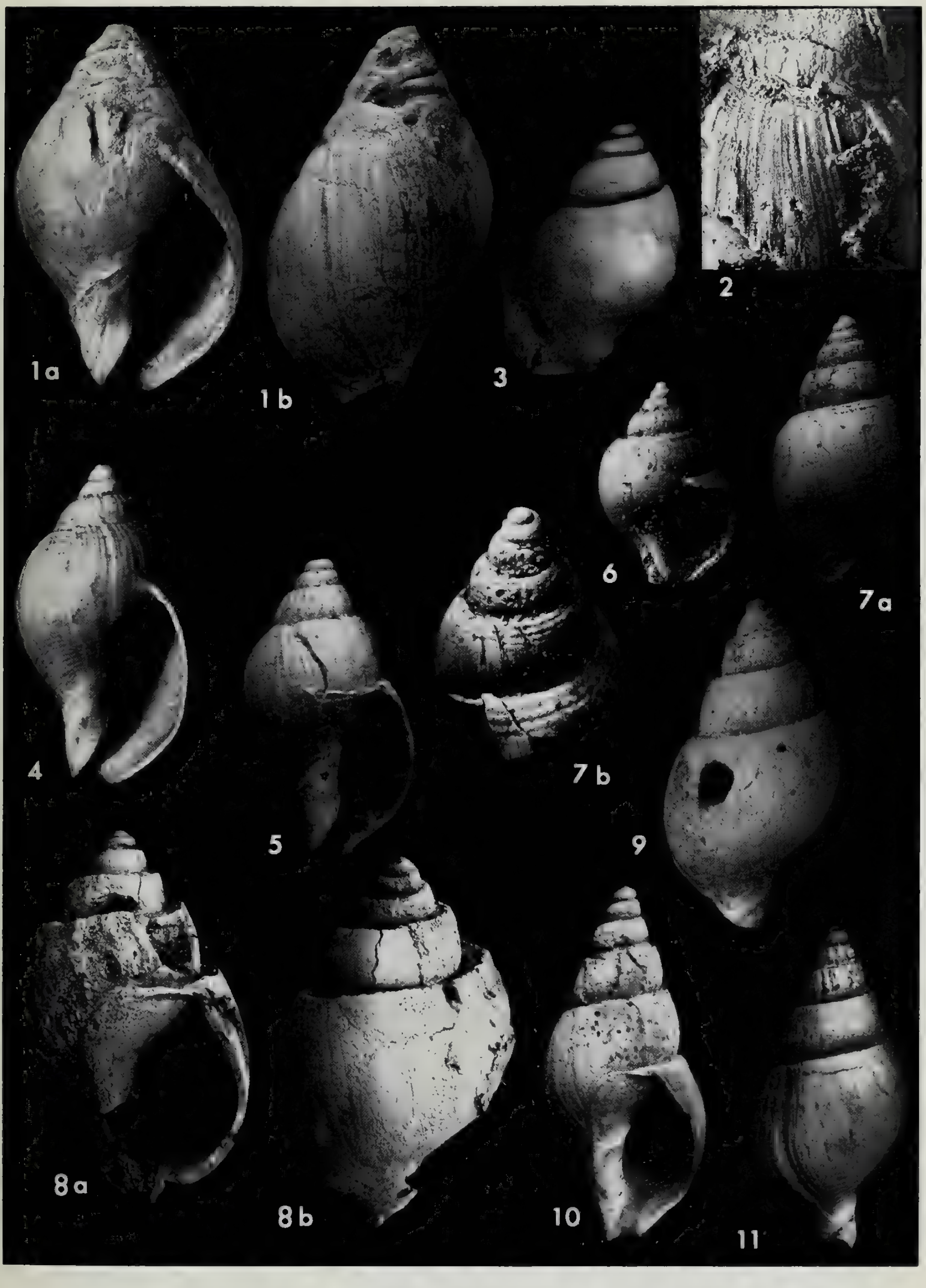

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PLATE 6

Figs 1–4

Whitecliffia suturosa (Nyst) p. 204

Figs 1a, b. GG 19717 (*Ed*). Upper Eocene, late Priabonian, Middle Headon Beds, Royden, Hampshire, specimen referred to as *Cominella ventricosa* Edwards MS by Judd (1880 : 154) and by Keeping & Tawney (1881 : 116), and possibly as *Buccinum suturosum* (Nyst), by von Koenen (1867 : 83). ×3.

Figs 2–4. Lower Oligocene, Lattorfian, Latdorf, Germany (*Ed*).

Figs 2a, b. GG 19720/1. Specimen with relatively strong spiral grooving. ×3.

Fig. 3. GG 19720/2. Rear view of specimen with very weak spiral sculpture. ×3.

Fig. 4. GG 19719/2. Oblique view showing protoconch, form of suture and sculptural details. ×4.

Figs 5–10

Whitecliffia tumida sp. nov. p. 206

Upper Eocene, late Priabonian, Middle Headon Beds (*Venus* Bed), Whitecliff Bay, Isle of Wight.

Figs 5a, b. Holotype. GG 19722/1 (*Cu*). ×4.

Figs 6–10. Paratypes. (All (*Cu*) except fig. 9).

Figs 6a, b. GG 19722/3. Specimen with inflated body whorl, Fig. 6a ×3; Fig. 6b, showing collabral colour banding. ×2·7.

Fig. 7. GG 19722/6. Showing broad colour band on ramp, with narrow one below it. ×2·7.

Figs 8a, b. GG 19724. Small individual lacking strong axial sculpture on early whorls, Fig. 8a, ×5·5; Fig. 8b, ×5.

Fig. 9. (*Sedg. Mus., K&T*) C.29305. ×3.

Fig. 10. GG 19722/2. Juvenile shell showing paucispiral protoconch. ×11 (stereoscan).

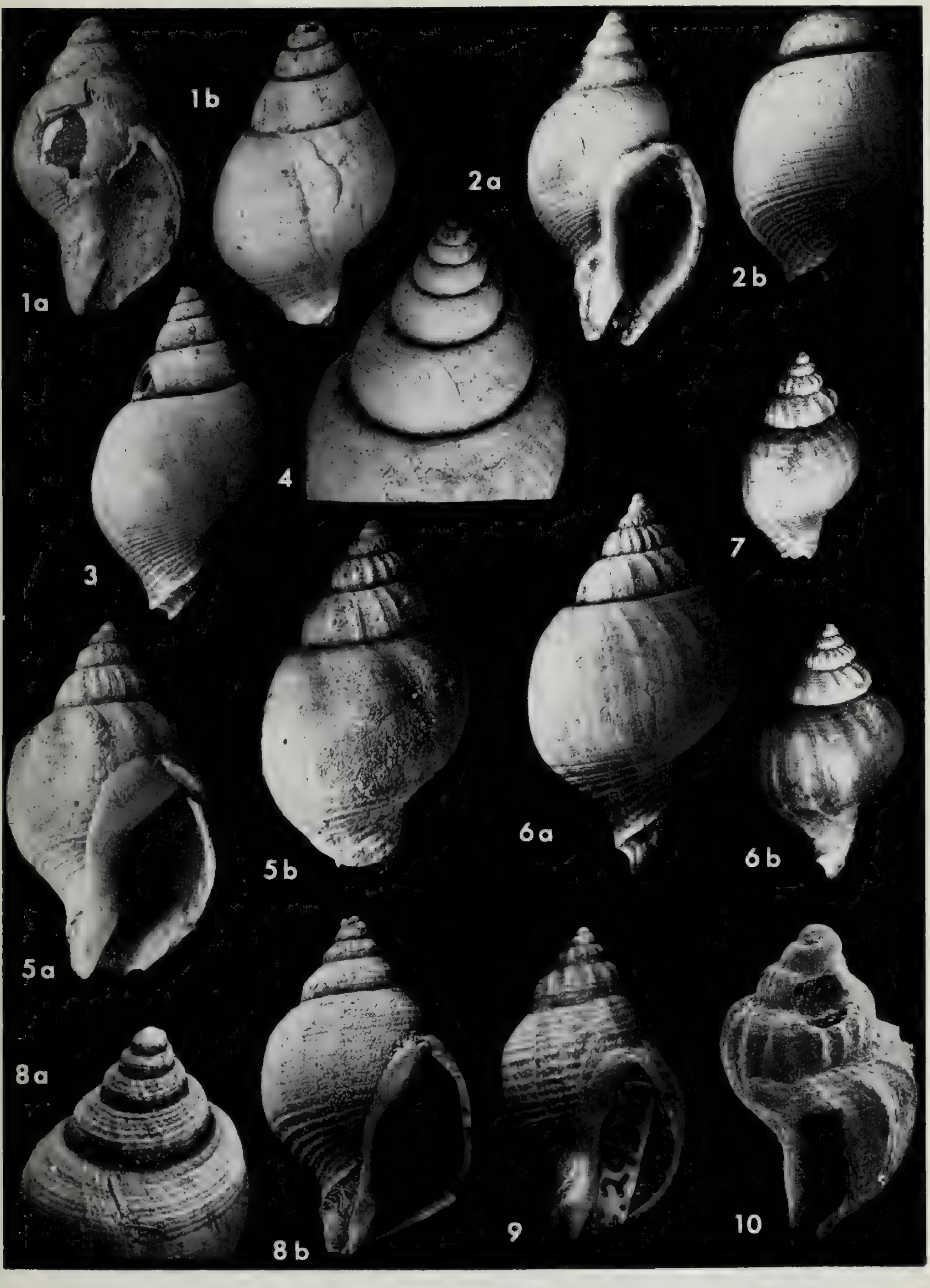
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PLATE 7

Figs 1–5

Colwellia flexuosa (Edwards) p. 210

Upper Eocene, Late Priabonian, Middle Headon Beds, Isle of Wight.

Figs 1a, b. Lectotype. GG 19709/1 (*Ed*). Colwell Bay. ×4.

Figs 2a–e. Paralectotype. GG 19709/3 (*Ed*). Colwell Bay, exceptionally large specimen; 2a, ×3; 2b, oblique view of fasciole, ×4; 2c, side view of outer lip, showing changes in growth lines with development of siphonal notch and peripheral sinus (compared with fig. 4), ×3; 2d, 2e, ultra-violet photographs showing colour banding. ×2.

Figs 3a–c. Paralectotype. GG 19709/4 (*Ed*). Colwell Bay, 3a, ×5; 3b, ×24 (stereoscan); 3c, ×27 (stereoscan).

Fig. 4. GG 19711 (*Nu*), *Venus* Bed, Colwell Bay, side view showing abrupt transition from relatively orthocline to very flexuous growth lines (compare with fig. 2c). ×3.

Figs 5a, 5b. GG 19713 (*Cu*), *Venus* Bed, Whitecliff Bay, juvenile specimen. ×6.

Figs 6–7

Colwellia auversiensis (Deshayes) p. 208

Middle Eocene, Auversian, Auvers, Paris Basin.

(*Deshayes Colln, EMP*), specimens probably belonging to the type series of *Buccinum auversiense* Deshayes (1865 : 498; 1866, pl. 94, figs 1–3), both ×2·5.

Figs 8, 9

Colwellia bretzi (Weaver) p. 208

Upper Eocene, Lower Cowlitz Formation, Vader, Washington State, U.S.A.

Fig. 8. GG 12783/1. (*Wr*) ×5.

Fig. 9. GG 12783/2 (*Wr*) ×16 (stereoscan).

Fig. 10

?Colwellia sp. p. 209

(*Bruce Martin Colln, CAS.*, Loc. 244). Upper Eocene, Tejon Group, Tejon Quadrangle, Kern County, California, U.S.A., east bank of Live Oak Creek about three quarters of a mile from its mouth or from the edge of the San Joaquin Valley, and about three miles due east of the mouth of Grapevine Canyon. Specimen referred to and figured as *Molopophorus striatus* (Gabb) by Dickerson (1915 : 65, pl. 8, fig. 6 given as fig. 7 in explanation thereof). ×6. (See also pl. 8.)

Fig. 11

Colwellia antiquata (Gabb) p. 208

(*U.Cal.* 15939, Loc.A-819), specimen described and figured as *Molopophorus antiquatus* (Gabb) by Vokes (1939 : 142, pl. 19, fig. 2), oblique view showing protoconch. ×6.

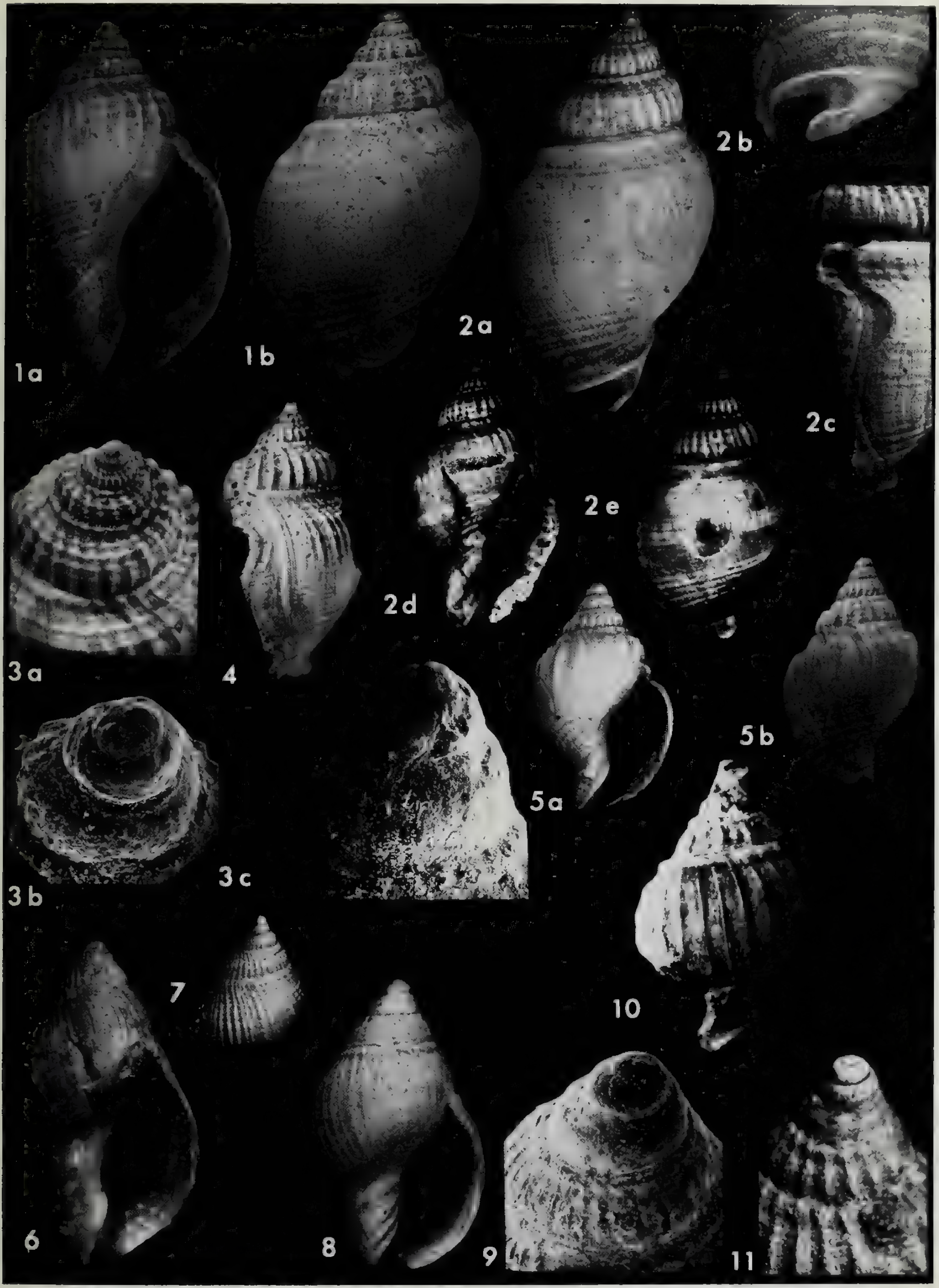
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PLATE 8

FIGS 1, 2

Molopophorus striatus (Gabb) p. 209

Type species of *Molopophorus*, Upper Eocene, Tejon Formation, Tejon, California.

FIG. 1a, b. Lectotype. (*ANSP* 4249) selected Stewart (1926 : 389, pl. 29, fig. 14), 1a ×9; 1b ×6.
FIG. 2. (*U.Cal.* 7182) Showing sculpture on spire. ×9.

FIGS 3, 4

Brachysphingus gibbosus Nelson p. 209

Palaeocene, Martinez Formation, Ventura County, California (ex *U.Cal.*).

FIG. 3. G 72721. Oblique view showing growth lines reversed at suture. ×1·7.
FIG. 4. GG 12834/1. Section showing absence of columellar plait. ×2.

FIGS 5–7

Keepingia gossardi (Nyst) p. 212

Middle Oligocene, Rupelian.

FIGS 5a, b. GG 19739/1. Etampes, France. ×2·5.
FIG. 6. (*EMP*) unlocalised young shell. ×16 (stereoscan).
FIG. 7. GG 19748/1. ?Klein Spauwen (type locality), Belgium. ×3.

FIG. 8

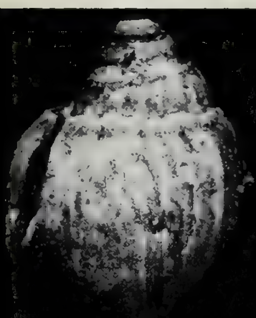
Keepingia bolli (Beyrich) p. 212

GG 19749/1 (*Wr*), Upper Oligocene, Chattian, Almatil near Cassel, Germany. ×2.

FIG. 9

Keepingia cassidaria (Sandberger) p. 212

GG 19733/1 (*Wr*), Upper Oligocene, Chattian, Cyrenmergel, Sulzheim, Germany. ×4.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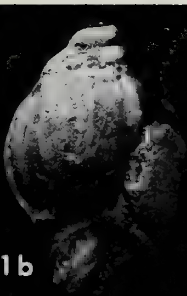
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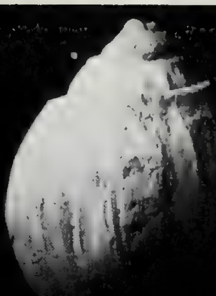
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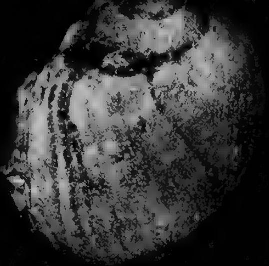
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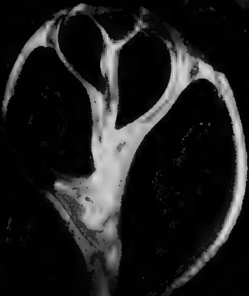
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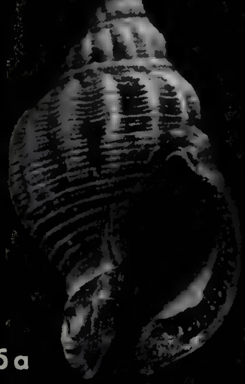
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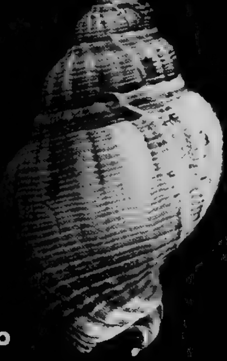
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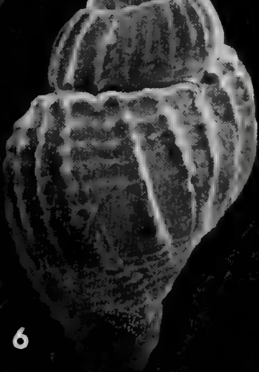
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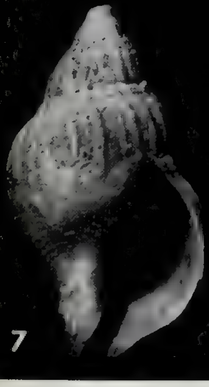
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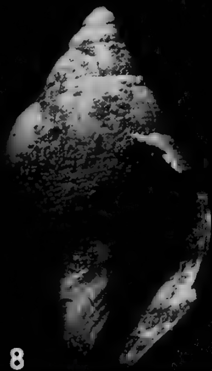
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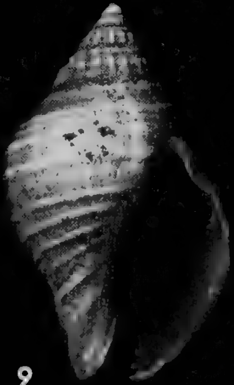
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PLATE 9

Figs 1–7

Thanetinassa bicorona (Melleville) p. 213

Palaeocene, Thanetian.

Figs 1–4. Châlons-sur-Vesle, France. (*L. Staadt Colln.*)
Fig. 1. GG 19357/1. ×3.
Fig. 2. GG 19357/3. ×4.
Fig. 3. GG 19357/2. Oblique view showing 'stromboid-like' notch in outer lip. ×4.
Fig. 4. GG 13357/4. Section showing form of columella. ×3.

Figs 5–7

Corbula Bed, Upper Thanet Sands, Bishopstone Gap, Herne Bay, Kent.

Fig. 5. GG 19741/1 (*Wr*). ×4.
Fig. 6. GG 19744 (*Ru*). ×3.

Figs 7a, b. G 60746 (*J. E. Cooper Colln.*). ×3.

Figs 8a, b

Buccinum montense Briart & Cornet p. 215

G 71604 (*Chavan Colln.*). Palaeocene, Montian, Belgium.

Fig. 8a. ×9.
Fig. 8b. Oblique view of fasciole. ×15.

Fig. 9

Nassarius arcularius (Linné) p. 181

Type species of *Nassarius*, Recent, Indo-Pacific. BMZD.19716 (*Hugh Cuming Colln*) I. of Ticao, Philippines, on reef, figd. Reeve (1853), pl. 4, fig. 25a). ×1·5.

Fig. 10

Strepsidura turgida (Solander) p. 190

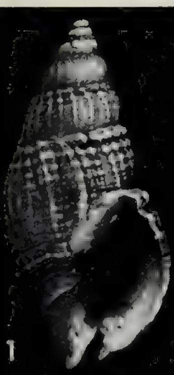
Type species of *Strepsidura*, GG 19750 (*StJB*), Upper Eocene, Bartonian, Barton Beds, Barton-on-Sea, Hampshire. ×2.

Figs 11a, b

Cominella testudinea (Lamarck) p. 180

Type species of *Cominella*, *BMZD*.1844.7.29.36 New Zealand.

Fig. 11a. ×2.
Fig. 11b. Oblique view of fasciole. ×5.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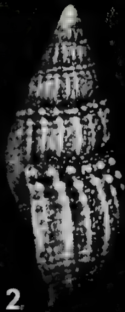
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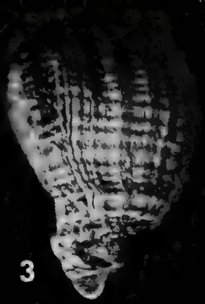
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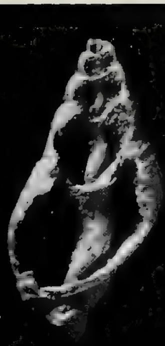
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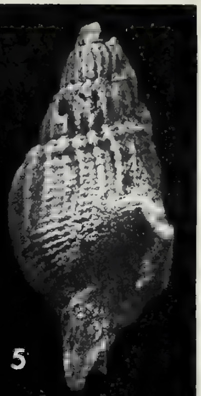
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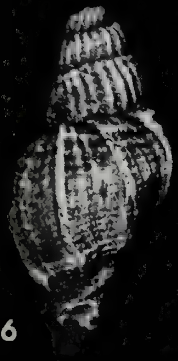
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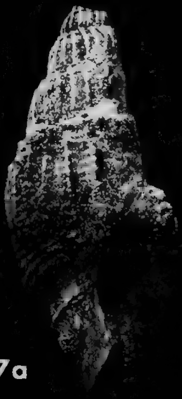
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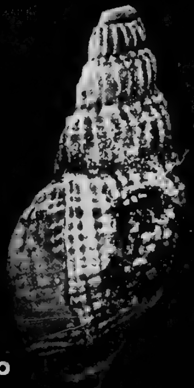
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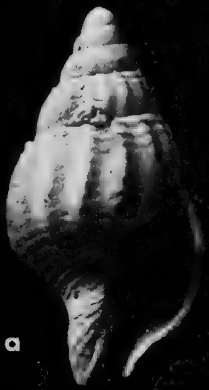
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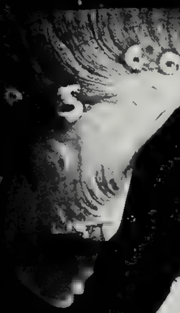
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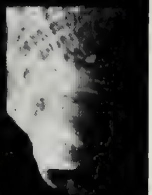
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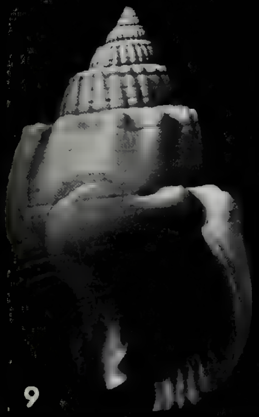
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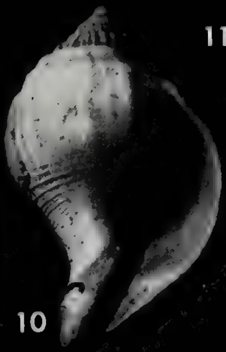
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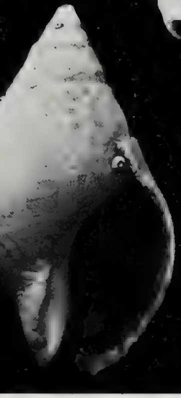
11a

A LIST OF SUPPLEMENTS TO THE GEOLOGICAL SERIES OF THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY)

1. Cox, L. R. Jurassic Bivalvia and Gastropoda from Tanganyika and Kenya. Pp. 213; 30 Plates; 2 Text-figures. 1965. £6.
2. El-Naggar, Z. R. Stratigraphy and Planktonic Foraminifera of the Upper Cretaceous—Lower Tertiary Succession in the Esna-Idfu Region, Nile Valley, Egypt, U.A.R. Pp. 291; 23 Plates; 18 Text-figures. 1966. £10.
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PALAEOZOIC CORAL FAUNAS FROM VENEZUELA, II. DEVONIAN AND CARBONIFEROUS CORALS FROM THE SIERRA DE PERIJÁ

URAL HISTO

C. T. SCRUTTON

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 23 No. 4
LONDON : 1973

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BRITISH MUSEUM
8 JUN 1973
NATURAL HISTORY

BY

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PALAEOZOIC CORAL FAUNAS FROM VENEZUELA, II. DEVONIAN AND CARBONIFEROUS CORALS FROM THE SIERRA DE PERIJÁ

By C. T. SCRUTTON

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SYNOPSIS

Rugose and tabulate corals of Middle Devonian, and Lower Pennsylvanian age are described from localities in the northern part of the Sierra de Perijá, western Venezuela. The Palaeozoic stratigraphy of the area is briefly reviewed and the ages and relationships of the coral faunas are discussed. The new taxa *Bowenelasma typa* gen. et sp. nov., *B. breviseptata* sp. nov., *Amplexizaphrentis sutherlandi* sp. nov., *Briantelasma oliveri* sp. nov. and *Heliophyllum wellsi* sp. nov., as well as species of *Stereolasma*, ?*Stewartophyllum*, *Syringaxon*, *Heterophrentis* (*H*.), *Cylindrophyllum*, *Durhamina*, *Plasmophyllum* and *Favosites* are described.

I. INTRODUCTION

This is the second of two papers describing rugose and tabulate corals from the Palaeozoic rocks of the Venezuelan Andes. The first paper (Scrutton 1971) dealt with Silurian and Permo-Carboniferous corals from the Mérida Andes. This paper describes material of Devonian and Carboniferous ages from localities in the northern Sierra de Perijá (see Fig. 1), some 300 km to the north-west and close to the Venezuelan-Colombian border.

The bulk of the material was collected during 1959 by Dr J. M. Bowen (then Compañia Shell de Venezuela) but the opportunity is taken here to revise in addition the small samples of corals collected by C. W. Yeakel, P. W. McFarland and R. A. Liddle in 1924 (described by Weisbord 1926) and by R. A. Liddle in 1942 (described by Wells 1943) which came from the same or nearby sections. The richest fauna is one of upper Onesquethaw age (considered equivalent to the early Middle Devonian) in terms of the eastern North American stages (see Oliver 1968, fig 1), represented by 14 of Bowen's samples and including most if not all of the older collections. A further three of Bowen's samples are also Devonian in age. The Devonian corals, which show very strong affinities with coral faunas of the same age in eastern North America, include sixteen species belonging to eleven genera; one genus and four species are new. Three of Bowen's samples contain corals which, with some supporting evidence, indicate probable Carboniferous ages. Three species, two of them new, belonging to two genera are involved. The material is housed in the Department of Palaeontology, British Museum (Natural History).

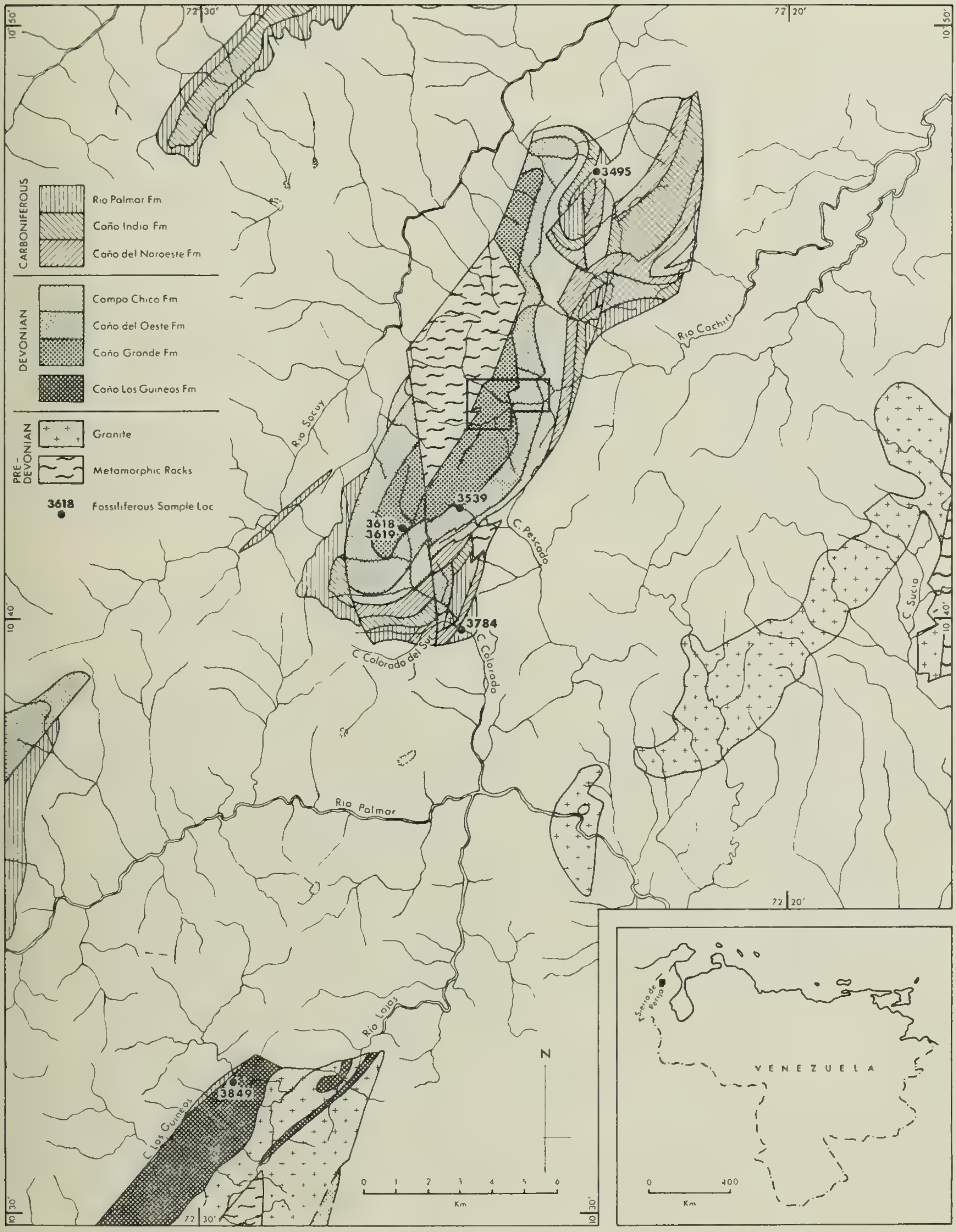
10°50'
72°30'
72°20'
CARBONIFEROUS
Rio Palmar Fm
Caño Indio Fm
Caño del Noroeste Fm
DEVONIAN
Campo Chico Fm
Caño del Oeste Fm
Caño Grande Fm
Caño Los Guineos Fm
PRE-DEVONIAN
Granite
Metamorphic Rocks
3618
Fossiliferous Sample Loc
3495
3539
3618
3619
3784
3849
Rio Socuy
Rio Cachiri
C. Pescado
C. Colorado del Sur
C. Colorado
C. Sucio
Rio Palmar
Rio Lajas
C. Los Guineos
10°40'
10°30'
N
0 1 2 3 4 5 6
Km
Sierra de Perijá
VENEZUELA
0 400
Km

FIG. 1. Geological map of the northern Sierra de Perijá showing sample locations (for further information see Appendix). The area covered in detail in Fig. 2 is outlined. Based on maps supplied by J. M. Bowen.

II. ACKNOWLEDGEMENTS

The author is most grateful to Dr J. M. Bowen (Shell International Petroleum Corporation), who collected most of the material, for discussions on the stratigraphy of the northern Sierra de Perijá and for permission to use information not yet published. Dr Bowen kindly made available the maps upon which Text-figs 1 and 2 are based. Acknowledgement is due to Compañia Shell de Venezuela for permission to describe Bowen's collection which they have presented to the British Museum (Natural History), and to Dr K. V. W. Palmer (Paleontological Research Institution) who has facilitated the loan of material in her care.

Dr W. J. Oliver Jr. (U.S. Geological Survey) has kindly read the systematic section of the manuscript and has contributed valuable discussion and information concerning eastern North American coral faunas of Devonian age. Dr J. G. Johnson (Oregon State University) has made valuable comments on the Devonian brachiopod faunas associated with the corals.

R. F. Wise and P. J. Green (British Museum (Natural History)) have respectively prepared and photographed material for this paper. E. Lawson (Department of Geology, University of Newcastle upon Tyne) drafted the originals of Text-figs 1–3, 5, 6, 8, 9 and 11.

III. PALAEOZOIC STRATIGRAPHY OF THE NORTHERN SIERRA DE PERIJÁ

The basic framework of the Palaeozoic stratigraphy of the northern Sierra de Perijá was first established by R. A. Liddle and his co-workers during expeditions along the course of the Río Cachirí in 1924 and 1942. The results were published in some detail in Liddle, Harris & Wells (1943). Subsequently a number of papers have been published referring to the area (including Sutton 1946, Hea & Whitman 1960 and Miller 1962) and knowledge of the Devonian sections was summarised by Weisbord (1968). These contributions, however, did not substantially modify the stratigraphical results of Liddle's expeditions. The most significant advance in the understanding of the Palaeozoic successions is due to J. M. Bowen's work in the northern Sierra de Perijá during 1959 when the material described in this paper was collected. Both the geological map (Figs 1, 2) and the stratigraphic successions (Fig. 3) reproduced here are based on the results of his work (Bowen 1972).

From the first descriptions of the rich macrofauna yielded by the oldest fossiliferous rocks of the area, published by Weisbord (1926), the strong resemblance to faunas of the upper Lower Devonian to lower Middle Devonian Onesquethaw interval in eastern North America was recognized. Liddle, in Liddle, Harris & Wells (1943) later distinguished three formations of Devonian age in the Río Cachirí section, the Caño Grande Formation, the Caño del Oeste Formation and the Campo Chico Formation in order of decreasing age, grouped together as the Río Cachirí Series (Cachirí Group of Sutton 1946 : 1634). The rich invertebrate fauna was confined to the Caño Grande Formation and Liddle described both the other formations as unfossiliferous (Liddle, Harris & Wells 1943 : 286, 289), although as Weisbord (1968 :

221) pointed out, Liddle records in his list of samples (Liddle, Harris & Wells 1943 : 313, sample 37) *Heliophyllum halli* and '*Heterophrentis venezuelense*' apparently *in situ* on the Caño del Oeste Formation outcrop in the Caño del Oeste section. In view of Liddle's statement in the text and the fact that Bowen's more extensive collections from the Caño del Oeste Formation do not contain these corals, it seems likely that sample 37 was in fact a displaced raft from the Caño Grande Formation such as are known to occur on this section. An even more anomalous situation, however, surrounds the original collection of fossils described by Weisbord (1926) and collected in 1924 by C. W. Yeakel in the company of P. W. McFarland and Liddle. According to Liddle (Liddle, Harris & Wells 1943, map) and Weisbord (1968 : 217) the collection was taken in the Caño del Norte about 4·5 km north of the Río Cachirí from the upper part of the Caño Grande Formation. That the fauna is of Caño Grande aspect can hardly be doubted, but Bowen (1972; Fig. 4) records no outcrop of this formation in, or even close to the Caño del Norte. In fact the difference between Liddle's and Bowen's maps of this particular section is most striking. Weisbord (1926 : 223) does record that 'the majority of our fossils were collected from float' and this may be the explanation. Alternatively, it is possible, in this sort of country, that the site of the collection was wrongly located (*fide* Bowen). Unfortunately no definite solution

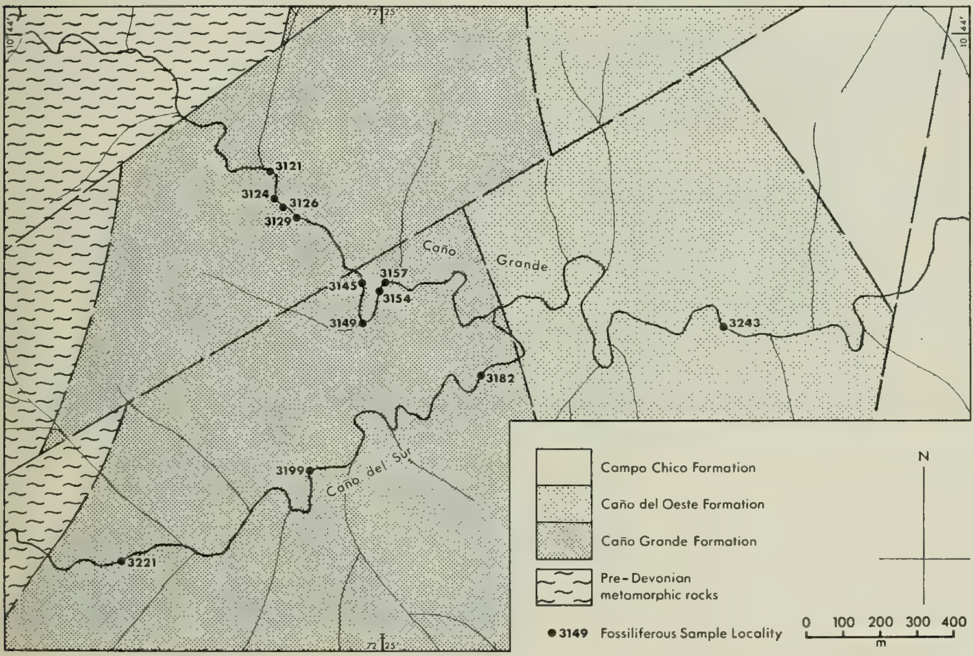
72°25'
10°44'
3121
3124
3126
3129
Caño Grande
3157
3145
3154
3149
3243
3182
3199
Caño del Sur
3221
72°25'
Campo Chico Formation
Caño del Oeste Formation
Caño Grande Formation
Pre-Devonian metamorphic rocks
● 3149 Fossiliferous Sample Locality
N
0 100 200 300 400
m

FIG. 2. Geological map of the upper reaches of the Río Cachirí, Sierra de Perijá showing sample locations (for further information see Appendix). The area covered here is indicated in Fig. 1. Based on maps supplied by J. M. Bowen.

to this problem seems possible at the moment and in this paper Yeakel's collection is considered as most likely to have originated from a displaced raft or possibly faulted slice of Caño Grande Formation in the Caño del Norte.

Bowen (1972) has recognized a fourth division of the Devonian Río Cachirí Group in the Sierra de Perijá. This, the Caño Los Guineos Formation of the Río Lajas area, he considers to be lower in the sequence than the Caño Grande Formation although the two formations do not crop out in the same sections. They have a very similar macrofauna and both formations are dated as Lower Devonian (Emsian, equivalent to the middle Onesquethaw) mainly on the basis of brachiopods although an early Middle Devonian age (upper Onesquethaw) is considered more likely here (see p. 230–31). Bowen has also collected a fossil suite dominated by brachiopods from the Caño del Oeste Formation, previously not satisfactorily dated, from which he deduces a lower Middle Devonian age. Finally, the highest, Campo Chico Formation has yielded palynomorphs indicating a Middle to Upper Devonian (probably Frasnian) age (Bowen 1972). The Devonian corals, discussed in detail in the following sections, come mainly from the Caño Grande Formation, for which they suggest an upper Onesquethaw age.

Liddle (Liddle, Harris & Wells 1943 : 290) assigned all the Permo-Carboniferous 'red-bed' sequence and overlying crinoidal limestones in the Río Cachirí section to the Palmarito Formation of Christ (1927). Bowen (1972) has considerably modified this succession, recognizing in it the lithological units described by Arnold (1966) from the Permo-Carboniferous of the Mérida Andes, about 300 km to the south-east. The basal development of red-beds Bowen assigns to the Sabaneta Group. Equivalent lower and upper divisions are recognized by both Arnold and Bowen which the

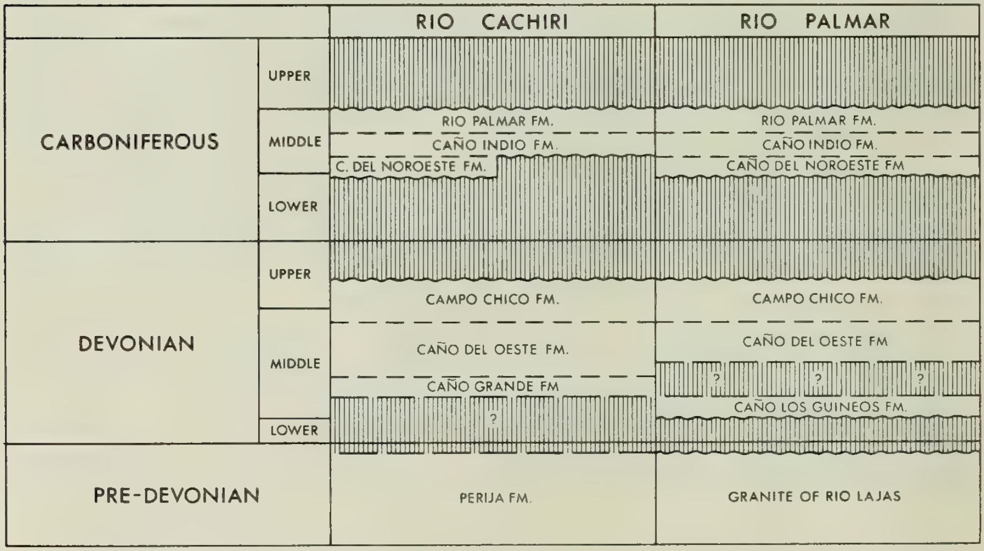
RIO CACHIRI
RIO PALMAR
CARBONIFEROUS
UPPER
MIDDLE
LOWER
RIO PALMAR FM.
CAÑO INDIO FM.
C. DEL NOROESTE FM.
RIO PALMAR FM.
CAÑO INDIO FM.
CAÑO DEL NOROESTE FM
DEVONIAN
UPPER
MIDDLE
LOWER
CAMPO CHICO FM.
CAÑO DEL OESTE FM.
CAÑO GRANDE FM
?
CAMPO CHICO FM.
CAÑO DEL OESTE FM
? ? ?
CAÑO LOS GUINEOS FM.
PRE-DEVONIAN
PERIJA FM.
GRANITE OF RIO LAJAS

FIG. 3. Devonian and Carboniferous successions in the northern Sierra de Perijá (after Bowen 1972). For comments see text.

latter erects as new formations. The Caño del Noroeste Formation below (equivalent to Arnold's lower clastic member) contains a fauna of fusulinids, brachiopods and palynomorphs indicating a lower Middle Carboniferous Namurian to Lower Westphalian age (Lower Pennsylvanian) according to Bowen (1972) whilst the Caño Indio Formation above is unfossiliferous. The age of the Caño Indio Formation is fixed as low in the Pennsylvanian, however, by the dating of the overlying Río Palmar Formation. This contrasts with the as yet poorly dated Sabaneta Group (Sabaneta Formation of Arnold 1966) of the Mérida Andes, the type area, where fossiliferous marine horizons are not known. Here, Arnold (1966 : 2371–2372) records a possible Permian age for the higher parts of the Sabaneta Group on the evidence of spores.

The Río Palmar Formation is a thick carbonate sequence conformably succeeding the Sabaneta Group. It is dated late Middle Carboniferous (late Lr. Pennsylvanian) on the basis of fusulinids and palynomorphs (Bowen 1972) and is the only level in the Permo-Carboniferous from which corals are described in this paper. This new formation is not represented in the Mérida Andes (Bowen 1972) where Arnold (1966 : 2373, 2377) records the Sabaneta Group grading upwards through a transitional zone into the Palmarito Formation. In the northern Sierra de Perijá, the typical facies of the Palmarito Formation, which is absent from the Río Cachirí area but crops out further south, comes in unconformably above the Río Palmar Formation. According to Bowen (1972), the whole of the Upper Pennsylvanian is apparently missing here, with the Palmarito Formation yielding Wolfcampian fusulinids. In the Mérida Andes, however, the rich marine fauna of the Palmarito Formation suggests that the late Pennsylvanian as well as the early Permian may be represented (Arnold 1966 : 2378; Scrutton 1971 : 189). Thus it would appear that the distinctive carbonate facies of the Río Palmar Formation is the lateral equivalent of rocks of upper Sabaneta or, less likely, lower Palmarito type to the south-east.

Between the Palmarito Formation and the Lower Cretaceous Río Negro Formation, Bowen (1972) has described a succession of pyroclastics, lavas and terrestrial sediments of ?Permian to Jurassic age. As no material from these younger rocks is described in this paper, they are not considered further here.

IV. AGES AND RELATIONSHIPS OF THE CORAL FAUNAS

The extent of previous work on South American Palaeozoic coral faunas was briefly reviewed by Scrutton (1971 : 190). Two papers refer to Devonian corals from the northern Sierra de Perijá, those of Weisbord (1926) and Wells (1943). Weisbord described the material collected by C. W. Yeakel in 1924 and Wells revised the corals on the basis of further collections made by R. A. Liddle in 1942. In both collections, the corals were all from the Caño Grande Formation of the Río Cachirí area. J. M. Bowen's much more extensive collections from a wider area in the northern Sierra de Perijá have more than doubled the species list for the Caño Grande Formation as well as yielding small coral faunas from three further horizons. The compositions of the faunas are listed in Table 1 and are discussed below in ascending stratigraphical order.

TABLE I

Composition of coral faunas from the Río Cachirí Group (Devonian) and Río Palmar Formation (Carboniferous) of the Sierra de Perijá.

Species	Río Cachirí Group			Río Palmar Fm.
	Caño Los Guineos Fm.	Caño Grande Fm.	Caño del Oeste Fm.	
Stereolasma sp.	×			
Syringaxon sp.	×			
Heliophyllum halli	×	×		
H. wellsi		×		
Heterophrentis (*H.*) *simplex*	×	×		
H. (*H.*) *venezuelensis*		×		
Plasmophyllum secundum americanum		×		
P. sp.		×		
Acinophyllum vermetum		×		
Briantelasma oliveri		×		
Bowenelasma typa		×		
B. breviseptata		×		
Favosites venezuelensis		×		
F. arbuscula		×		
Cylindrophyllum elongatum		—— ?	——	
?*Stewartophyllum* sp.			×	
Hadrophyllum sp.			×	
Amplexizaphrentis sutherlandi				×
?*Durhamina* sp.				×
Durhamina sp. nov.				?

(a) *Río Cachirí Group*

(i) *Caño Los Guineos Formation.* A small fauna of four different corals only is available from this formation. Its composition suggests affinities with Middle Devonian coral faunas of eastern North America where *Heliophyllum halli* Edwards & Haime in particular is characteristic of the Onondaga Limestone and Hamilton Group of New York and their equivalents elsewhere. *Stereolasma* appears to have a similar, though less well documented range and *Heterophrentis* (*H.*) *simplex* (Hall) has been recorded so far only from horizons of Hamilton age in New York and the Ohio Valley (see Oliver 1968, fig. 1 for a correlation chart of the eastern North America Devonian).

Bowen (1972) lists other fossils, principally brachiopods, from the Caño Los Guineos Formation which he takes to indicate an upper Lower Devonian (Emsian) age. There is some doubt, however, as to the reliability of this brachiopod fauna in distinguishing between a late Lower and an early Middle Devonian age (J. G. Johnson, pers. comm.). This matter is discussed more fully in the following section on the Caño Grande Formation which has yielded similar but richer coral-brachiopod faunas. In view of the ambiguity of the brachiopod evidence, the affinities of the coral fauna suggest that an upper Onesquethaw age (early Middle Devonian) is more likely than a late Lower Devonian age for this formation.

(ii) *Caño Grande Formation.* The principal Onondaga—Hamilton species present in this much richer coral fauna are *Heliophyllum halli*, *Heterophrentis* (*H.*) *simplex*, *Plasmophyllum secundum americanum* (Edwards & Haime) and *Favosites arbuscula* Hall. In addition, *Acinophyllum vermetum* (Weisbord)[1] is considered to agree in all its essential characteristics with *A. stramineum* (Billings) from the lower part of the Onondaga Limestone of Ontario (Oliver, in preparation) and *Cylindrophyllum elongatum* Simpson, which comes either from the Caño Grande Formation or the overlying Caño del Oeste Formation, is also found at the same horizon in New York. This evidence would clearly suggest an upper Onesquethaw (lower Middle Devonian) age for the Caño Grande coral fauna. Also present, however, is a new species of *Briantelasma.* This genus has previously been recorded from rocks of Silurian (?Wenlock) and Lower Devonian (Helderberg) age in eastern North America (Oliver 1960a, b, 1963) and is the only element in the coral fauna not previously recorded from the Middle Devonian. The new genus *Bowenelasma* provides no direct evidence but its general characteristics relate it more to *Briantelasma* and Silurian streptelasmatids rather than to typical Middle Devonian members of the family. It should be stressed, however, that there is no sign of typical eastern North American middle Onesquethaw corals in the Venezuelan fauna.

Bowen (1972) lists a brachiopod fauna from the Caño Grande Formation, very similar to that in the Caño Los Guineos Formation, which he takes to indicate a late Lower Devonian age. He infers that this is supported by palynomorphs. As previously noted (p. 230), however, Dr J. G. Johnson (pers. comm.) doubts that confidence can be placed in the brachiopod fauna at the moment to distinguish between a middle and an upper Onesquethaw age (that is, late Lower Devonian and early Middle Devonian as currently understood in North America). In particular, Johnson notes that *Eodevonaria* has been collected from rocks of upper Onesquethaw age, and he regards the upper limits of the range of *Leptocoelia* to be uncertain. Both genera have been taken to indicate a Lower Devonian horizon. He also draws attention to the occurrence of *Tropidoleptus* (Morales 1965) and common *Pentagonia* and *Spinulicosta*, all more suggestive of an upper Onesquethaw than a Lower Devonian age, in the Floresta fauna of Colombia, with which the Venezuelan faunas have much in common. Johnson thinks it likely that these South American occurrences represent an overlap of late Lower and early Middle Devonian forms. Dr L. Nijssen (pers. comm.), who made the palynological determinations, also has reservations about distinguishing between an Emsian and an early Eifelian age on the basis of the flora.

Although much revision of the North American coral faunas is necessary, Oliver (1968 : 741) clearly indicates that an important break in the sequence of coral assemblages there occurs between the middle and upper Onesquethaw. In this light, the strong affinities of the coral fauna with faunas of upper Onesquethaw age in eastern North America suggests that the Caño Grande Formation should be dated upper Onesquethaw (early Middle Devonian) rather than middle Onesquethaw at the present time.

---

[1] As Dr W. J. Oliver Jr. has a review of this species in preparation it is not described in the systematic section of this paper.

The affinities between the Venezuelan and eastern North American coral faunas indicates that the two areas must have formed part of the same province in early Middle Devonian time. The presence of *Bowenelasma* and some species endemic to Venezuela suggests that north–south migration may have been partially restricted in some way, although these corals may be recorded from eastern North America in the future.

(iii) *Caño del Oeste Formation.* This formation appears to be poor in corals although it has provided a fairly varied fauna of brachiopods and molluscs which are listed by Bowen (1972). One specimen each of ?*Stewartophyllum* sp. and *Hadrophyllum* sp. indicate a tentative Middle Devonian age, whilst the brachiopods have been more precisely dated as early Middle Devonian.

Although the specimen of *Cylindrophyllum elongatum*, which comes from a slipped block, is listed by Bowen (1972) with the Caño del Oeste fauna, Bowen has informed the writer that the block compared lithologically with the Caño Grande Formation outcropping further up the Caño Pescado and may well have come from that formation. If the block did originate from the Caño del Oeste Formation, however, then it would be from near the base, whereas the rest of the fauna, providing evidence for the age, derives from the very top of the formation.

(b) *Río Palmar Formation*

This formation has also yielded two corals among a rather limited invertebrate fauna. *Amplexizaphrentis sutherlandi* sp. nov. and ?*Durhamina* sp. indicate a general Carboniferous age and compare most closely with North American cordilleran species. The other faunal elements provide more precise information and indicate a late Lower Pennsylvanian age.

Durhamina sp. nov. is known only from a loose block whose stratigraphic relationships are obscure. Of the known stratigraphy, it is most likely to have come from the Río Palmar Formation which is where Bowen (1972) lists it as 'durhaminido gen. and sp. nov.'. Possible Mississippian brachiopods were reported from the same block, however, and it may represent an horizon as yet not recognized *in situ* in the stratigraphic sequence.

V. SYSTEMATIC DESCRIPTIONS

The terminology used in the following descriptions is that proposed by Smith (1945 : 4–9) and Moore, Hill & Wells (1956) unless otherwise indicated.

All the material collected by Bowen is now housed in the Department of Palaeontology, British Museum (Natural History). The registered numbers for these specimens are prefixed R and in each case the number of the sample in which the specimen was collected is given in parentheses after the registered number. The locations of Bowen's samples are plotted on Text-figs 1 and 2 and full details are given in the Appendix.

The sources of other material described below are indicated by the following abbreviations: PRI—Paleontological Research Institution, Ithaca, N.Y.; NYSM—New York State Museum, Albany, N.Y.

Order RUGOSA Edwards & Haime 1850
Suborder STREPTELASMATINA Wedekind 1927
Superfamily **CYATHAXONIICAE** Edwards & Haime 1850
Family **LINDSTROEMIIDAE** Počta 1902

1971 Lindstroemiidae; Scrutton: 192, *cum syn.*

Discussion. The family concept was reviewed by Scrutton (1971 : 192).

Genus ***STEREOLASMA*** Simpson 1900

1900 *Stereolasma* Simpson: 205.
1941 *Stereolasma* Busch: 395.
1949 *Stereoelasma* Stumm: 7.
1962 *Stereolasma* Stumm: 234.
1965 *Stereolasma* Stumm: 14.

Diagnosis. Small ceratoid to trochoid corals. Major septa fuse in the axis to form, with or without additional sclerenchyme, a prominent axial pillar. Minor septa short, usually contratingent. Peripheral stereozone narrow. Cardinal fossula narrow, poorly developed. Tabulae complete or incomplete, strongly arched with a flat or slightly depressed axial area. No dissepiments.

Type species (by original designation). *Streptelasma rectum* Hall 1876, pl. 19, figs 1–13 in part ?=*Strombodes*? *rectus* Hall 1843 : 210, text-fig. 87, 5 on p. 209, and no. 48, fig. 5 on p. 44 of tables. Middle Devonian, Hamilton Group; western New York State, U.S.A.

Discussion. Reference should be made to Stumm (1949 : 7) and Stumm & Watkins (1961 : 445) for comments on and a redescription of *Stereolasma rectum.*

Stereolasma sp.

(Pl. 1, figs 6, 7)

Material. R45129 (3849). Caño Los Guineos; Caño Los Guineos Fm., early Middle Devonian (upper Onesquethaw).

Description. Small ceratoid coral, incomplete.

In the late neanic stage the mean diameter is 11 mm with 25 major septa. The lumen is completely infilled by laterally contiguous wedge-shaped major septa merging in the axial area with a core of sclerenchyme 3 mm in diameter. This core may be formed by irregularly intertwined septal ends but the structure is not clear. There are signs of rudimentary minor septa as wedges about 1 mm long between the major septa.

In the ephebic stage (Pl. 1, fig. 6) there are 25 major septa at a mean diameter of 14·5 mm. The major septa, except the cardinal septum, are 0·6–0·75 mm thick where they are very slightly waisted one-third of the way along their length from the periphery. The cardinal septum is notably thinner at 0·4 mm. The septa are thickest about two-thirds of their length to the axis where they become laterally contiguous. From this point they taper smoothly into the axis in a slight counter clockwise vortex maintaining contact with their neighbours. The septa are longest in the alar area where they all but meet in the axis. The counter and cardinal septa are shorter, however, each reaching only three-quarters of the radius, leaving a narrow axial gap about 4·5 mm long and 0·5 mm wide in the otherwise solid oval core of fused septal ends, 7 mm × 6 mm in size. The peripheral ends of the septa alternate with contratingent minor septa in a peripheral stereozone 1–1·2 mm thick. The minor septa generally appear as short thorny projections from the stereozone mainly in the counter quadrants where they are more free standing. The minor septa flanking the counter septum are 2 mm long and they decrease in size round towards the cardinal septum near which they are 1·5 mm long. The minor septa contratingent on the major septa immediately flanking the cardinal septum, however, are again 2 mm long. Septal microstructure consists of an irregular structureless core embedded in calcite showing growth lamellae running at a very low angle to the septal faces axially and inward towards the core.

In the longitudinal section (Pl. 1, fig. 7), cut between the two sections described above, the lumen is infilled with septal material except for two small peripheral areas. The septal material shows bowl-shaped laminations, notched in the axis, which are interpreted as growth-lines. In the smaller of the two voids, part of a tabula can be seen curving upward and axially from the peripheral stereozone. There are no dissepiments.

The specimen contains circular borings, 0·8–1·1 mm in diameter, of unknown origin.

Discussion. This specimen appears to compare most closely in size and structure with the type species of *Stereolasma*, *S. rectum* (Hall) from the Middle Devonian Hamilton Group of eastern North America as illustrated by Simpson (1900, figs 16–18) and Stumm & Watkins (1961, pl. 58, figs 1–16). *S. rectum*, however, has much thinner skeletal elements and less well developed minor septa except for the counter-lateral minor septa which are strongly accelerated. The Venezuelan specimen may belong to a new species but further material is required to confirm this.

Genus ***STEWARTOPHYLLUM*** Busch 1941

1941 *Stewartophyllum* Busch: 393.
1949 *Stewartophyllum* Stumm: 9.
?1965 *Stewartophyllum* Federowski: 344.

Type species (by original designation). *Amplexus intermittens* Hall 1876; pl. 32, figs 8–15. Middle Devonian, Hamilton Group; Moscow, N.Y., U.S.A.

Diagnosis. Small subcylindrical to trochoid corals. Major septa dilated and extending to axis where they fuse in neanic stage, withdrawn from axis in ephebic stage. Cardinal fossula present. Minor septa very short or absent. Tabulae complete and incomplete, flat axially, variably orientated peripherally. No dissepiments (based on Stumm 1949 : 9 and Stumm & Watkins 1961 : 447).

Discussion. The type specimens of *S. intermittens* (Hall) have been redescribed by Stumm and Watkins (1961 : 447) who showed that three other species described by Busch should also be referred to Hall's species. The diagnosis for the genus given above takes account of this redescription.

?*Stewartophyllum* sp.

(Pl. 1, figs 4, 5)

Material. R45110 (3243). Caño Grande; Caño del Oeste Fm., early Middle Devonian.

Description. Small curved trochoid coral, about 25 mm high and 20 mm in maximum diameter.

In the late neanic-early ephebic stage, the lumen is almost entirely infilled. The septa occur in a single series up to 1·25 mm thick at the periphery and wedge-shaped, reaching between three and four-fifths of the way to the axis. They are arranged in an irregularly pinnate pattern and are mostly laterally contiguous with scattered very narrow gaps in the peripheral area between some septa. The axial ends of the septa merge into solid sclerenchyme completely infilling the axis, in which no structural details can be seen. The septal structure compares with that described as pseudotrabecular by Kato (1963, text-fig. 9e).

In higher sections a subtriangular cardinal fossula containing a short, thin cardinal septum, 4 mm long, is present on the convex side of the coral. There are slightly larger gaps between the septa and signs of tabulae can occasionally be seen. The axis of the coral is filled by a subcircular core of sclerenchyme 7 mm in diameter. As the subcalicular level is approached, the subtriangular cardinal fossula increases in size at the expense of the cardinal half of the core. The pinnate septal symmetry is also more regularly developed immediately below the calice. The diameter here is 16 mm with about 40 septa.

No longitudinal section is available.

Discussion. This single specimen is tentatively assigned to *Stewartophyllum*. It appears to have considerable structural similarity with *S. intermittens* (Hall) from the Middle Devonian Hamilton Group of eastern North America (see Stumm & Watkins 1961, pl. 58, figs 17–28, 37–39) although it is clearly not conspecific. Apart from the much higher septal number in the Venezuelan specimen, the large axial core of sclerenchyme makes even a congeneric assignment open to question. More material is required to assess the variability and significance of the axial core.

Genus *SYRINGAXON* Lindström 1882

1970 *Syringaxon* Sutherland: 1125.
1971 *Syringaxon* Scrutton: 194, *cum syn.*

DISCUSSION. See Scrutton (1971 : 194) for a diagnosis and full discussion of the status of this genus.

Syringaxon sp.

(Pl. 1, figs 1–3)

MATERIAL. R45130 (3849). Caño Los Guineos; Caño Los Guineos Fm., early Middle Devonian (upper Onesquethaw).

DESCRIPTION. Small conico-cylindrical coral with moderately developed septal grooves.

Coral circular in cross-section with a variably corrugated epitheca and a peripheral stereozone about 0·6 mm thick. In the mature stages the major septa are 0·13–0·2 mm thick midway along their length where they are very slightly waisted; the cardinal septum is the thinnest. They reach approximately seven-eighths of the radius towards the axis. The axial ends of the major septa are rhopaloid causing them to be laterally contiguous and to form, with a small amount of additional sclerenchyme, an aulos 2–2·5 mm in external diameter. In a subcalicular section (Pl. 1, fig. 1), the internal dimensions of the aulos are 1·2 × 0·9 mm. In a section approximately 1·5 mm below this (Pl. 1, fig. 2), the aulos is solidly infilled, possibly by sclerenchyme coating a tabula as the longitudinal section shows the aulos to be open for at least another 2·5 mm below the level of this section. The minor septa are approximately half the radius in length except for the counter-lateral minor septa which are equal in length to the counter septum. They are closely contratingent so that the lumen between a major septum and its contratingent minor may be closed at sub-calicular levels.

The longitudinal section is two-thirds infilled by septal material due to its being cut slightly off-centre. There is a very narrow open core in the distal part of the aulos containing irregularly spaced flat tabulae averaging 0·25 mm apart. In the interseptal loculi one tabula can be clearly seen, flat near the peripheral stereozone, and curving upwards towards the aulos. There are faint indications of what may be further tabulae but none can be positively identified as such.

The subcalicular section is about 6·8 mm mean diameter with 20 major septa and the section 1·5 mm below is 6·4 mm in mean diameter with 18 major septa.

DISCUSSION. This single specimen, although slightly larger in size at the same septal number, is quite similar to *S. arnoldi* Scrutton (1971 : 196) from rocks of Ludlovian age in the Mérida Andes of Venezuela. Further material is necessary, however, to determine the status of the Devonian specimen.

S. rudis (Girty 1897 : 299, pl. 2, figs 7, 8), from the Lower Devonian of North America, is in need of redescription and cannot be compared with the present material.

Family **HADROPHYLLIDAE** Nicholson 1889

1937 Palaeocyclidae Bassler: 189, *pars*.
1949 Hadrophyllidae Stumm: 4.
1955 Porpitidae Jeffords: 12, *pars*.
1956 Hadrophyllidae Hill: 262.
1961 Hadrophyllidae Fontaine: 69.
1969 Hadrophyllidae Sutherland & Haugh: 27.

TYPE GENUS. *Hadrophyllum* Edwards & Haime 1850 : 67.

DIAGNOSIS. Small, simple, discoid, patellate, button shaped or depressed turbinate corals. Major septa usually arranged in quadrants and cardinal and alar fossulae often strongly developed. Minor septa short and contratingent. Horizontal partitions (?tabulae) developed in some genera.

DISCUSSION. A brief resumé of the classification of this group of corals is given by Sutherland & Haugh (1969 : 28). For the moment, Hill's (1956 : 262) interpretation of the Hadrophyllidae is accepted and attention is drawn to the presence of what are probably tabulae in the specimen described below as *Hadrophyllum* sp. and in *Gymnophyllum wardi* Howell (see Sutherland & Haugh 1969 : 35).

Genus **HADROPHYLLUM** Edwards & Haime 1850

1850 *Hadrophyllum* Edwards & Haime: 67.
1851 *Hadrophyllum* Edwards & Haime: 357.
1937 *Hadrophyllum* Bassler: 197.
1952 *Hadrophyllum* Le Maitre: 41.
1955 *Hadrophyllum* Jeffords: 8.
1961 *Hadrophyllum* Fontaine: 69, *cum syn*.

DIAGNOSIS. Discoid to broadly trochoid. Cardinal septum in oval fossula; other cardinal quadrant septa pinnate and sub-parallel, counter quadrant septa more or less radially arranged with a long counter septum. Minor septa short. Horizontal partitions (?tabulae) may be developed.

TYPE SPECIES (by original designation). *Hadrophyllum orbignyi* Edwards & Haime 1851 : 357, pl. 6, figs 4, 4a. Devonian; Charleston Landing, Indiana and Clark County above Louisville, Kentucky, U.S.A.

DISCUSSION. The status of this genus has been discussed by Jeffords (1955 : 8). An amended diagnosis is given here to cover the occurrence of tabula-like structures in the specimen of *Hadrophyllum* described below.

Hadrophyllum sp.

(Pl. 1, fig. 8, Text-fig. 4)

MATERIAL. R49275 (3243). Caño Grande; Caño del Oeste Fm., early Middle Devonian.

Description. Small, broadly trochoid coral with smooth, slightly worn exterior. Calice not seen.

A single section at the ephebic stage shows the lumen largely infilled by thick septa arranged with striking pinnate symmetry. The septa are mostly between 1 and 1·4 mm in thickness peripherally. The counter and alar septa are longest, all three meeting in the axis. In the counter quadrants, the counter-lateral and next four metasepta are roughly equal in length and about three-quarters the length of the counter septum. The fifth and subsequent metasepta in the counter quadrants become progressively shorter and more wedge-shaped against the alar septa. On the cardinal side of the alar septa the first two metasepta are equal in length to the alar septa and the subsequent metasepta become progressively shorter and more wedge-shaped round towards the cardinal septum. The wall of the cardinal fossula appears to be the result of sclerenchyme coating the successive ends of the metasepta in the cardinal quadrants and is not formed by extra long metasepta flanking the short, 3·5 mm long, cardinal septum. Very narrow gaps, about 0·1 mm wide, separate the major septa in the peripheral area of the corallum. In several places the gaps are crossed by narrow bars that are probably tabulae. There are short triangular minor septa, about 1 mm long, inserted between nearly all the major septa. The septal formula is *C6A8K7A8C* at a mean diameter of 13 mm.

No longitudinal section is available.

Discussion. The general characters of this coral agree with those of the genus *Hadrophyllum* although it cannot be readily assigned to any described species. Comparison is made difficult as virtually no other species of *Hadrophyllum* has been

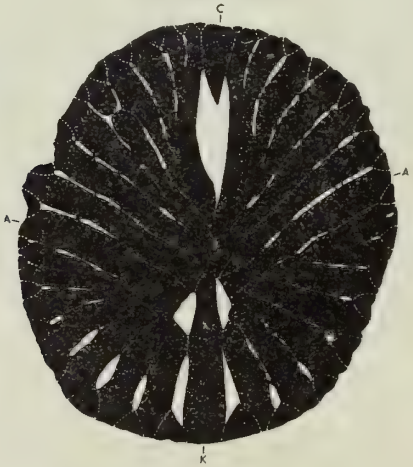

Fig 4. Septal arrangement in *Hadrophyllum* sp. (R49275). ×5.
C = cardinal septum; K = counter septum; A = alar septa.

studied with, or illustrated by, thin sections. The appearance of interseptal structures like tabulae in cross-section has never previously been recorded in a species of *Hadrophyllum* but this may also be due to a lack of thin section study. For example, rare tabulae have recently been recorded in thin sections of another member of the Hadrophyllidae, *Gymnophyllum wardi* Howell, by Sutherland and Haugh (1969 : 35).

Family **HAPSIPHYLLIDAE** Grabau 1928

1956 *Hapsiphyllidae* Hill: 267.
1964 *Hapsiphyllidae* Rowett & Sutherland: 46.

Genus ***AMPLEXIZAPHRENTIS*** Vaughan 1906

1906 *Amplexizaphrentis* Vaughan: 315.
1958 *Amplexizaphrentis* Sutherland: 44.
1962 *Amplexizaphrentis* Armstrong: 30.
1962 *Enniskillenia* Kabakovitch *in* Soshkina & Kabakovitch: 323.
1964 *Amplexizaphrentis* Rowett & Sutherland: 47.

DIAGNOSIS. Small, solitary, trochoid to ceratoid corals in which major septa may or may not unite around a conspicuous cardinal fossula. Septa commonly withdraw from axis in late stages of growth. Alar pseudofossulae usually well developed in early stages, but may become inconspicuous in ephebic stage. Tabulae usually complete, arched or flattened axially except where abruptly depressed in the fossula. No dissepiments. (After Rowett & Sutherland 1964 : 47).

TYPE SPECIES (see Opinion 854, I.C.Z.N. 1968). *Zaphrentis curvulena* Thomson 1881 : 223, 236. Lower Limestone Group, Lower Carboniferous; Brockley, near Lesmahagow, Lanarkshire, Scotland.

DISCUSSION. The status of the genus *Amplexizaphrentis* has been discussed by Sutherland (1958 : 44 *et seq.*) and his conclusions are accepted here. More recently a case to stabilize the generic name and type species was submitted to the I.C.Z.N. by Shrestha (1966), supported by Mitchell (1966) and approved by the Commission in Opinion 854. This effectively answered the comments on the validity of *Amplexizaphrentis* expressed by de Groot (1963 : 39).

According to Rowett & Sutherland (1964 : 51) *Barytichisma* (Moore & Jeffords 1945 : 131) is distinguished from *Amplexizaphrentis* 'primarily on the basis of the unusually wide peripheral stereozone'. They also note in the diagnosis for that genus that the septa are amplexoid and reach the axis immediately above the tabulae only. Weyer (1965 : 450) also laid emphasis on amplexoid septa in *Barytichisma* in maintaining the genus distinct from *Amplexizaphrentis*. If this distinction is accepted, the species described below seems to fall more naturally into *Amplexizaphrentis* than *Barytichisma* despite a tendency to amplexoid septa at all stages of growth. Certainly *A. sutherlandi* sp. nov. does not develop an unusually wide peripheral stereozone.

Amplexizaphrentis sutherlandi sp. nov.

(Pl. 1, figs 9–13, Text-fig. 5)

Derivation of name. After Dr P. K. Sutherland (University of Oklahoma).

Diagnosis. Curved ceratoid *Amplexizaphrentis* with cardinal fossula on concave side of corallum. Major septa thick, tending to amplexoid throughout ontogeny; 34 present in ephebic stage of holotype at 14 mm diameter. Minor septa rudimentary. Tabulae wide, flat with downturned edges, inclined strongly from the counter to cardinal side.

Holotype. R45127 (3784). Caño Colorado; Río Palmar Formation, Lr. Pennsylvanian.

Paratypes. R49291 (3784; ?distal end of holotype), R49292 (3784). Same locality and horizon as holotype.

Description. Curved ceratoid corals up to 60–70 mm long and about 25 mm maximum diameter (estimated because of crushing of the calice). The cardinal fossula is on the concave side of the corallum. Septal grooves weak or absent on a slightly rugate epitheca.

In the early neanic stage (Pl. 1, fig. 10) the septa are short and variably developed with a wide, open lumen. On the cardinal side a tabula is cut, on the upper surface of which the cardinal septum and several metasepta in the left cardinal quadrant are well developed. They are approximately 1·3 mm long and 0·5 mm wide at their bases, the cardinal septum being fractionally longer than the others. No septa can be distinguished in the zone where the tabula is in the plane of section and immediately below the tabula, in the alar areas, the septa are very short and thorn-like. In the counter area the counter septum is short and thin, about 1·3 mm long and 0·1 mm wide expanding to 0·5 mm wide where it merges into the thin peripheral stereozone. The flanking septa are similar in shape but become progressively shorter, from a maximum of 0·8 mm long, towards the alar areas. The mean diameter is 7 mm; 19 septa can be counted but there are probably 22 or 24 present at this level.

In a later neanic section (Pl. 1, fig. 11), approximately 2 mm higher than the first, the septa in the cardinal quadrants are much more strongly developed. The alar septa appear to meet across the axis of the corallum in a continuous band 0·5–0·8 mm thick and the metasepta in the cardinal quadrants are arranged in strongly pinnate groups. The ends of successive metasepta outline a large suboval cardinal fossula bisected by a long waisted cardinal septum extending to the axis. The metasepta in the cardinal quadrants are 0·4–0·6 mm thick peripherally and taper towards the axis. Where tabulae are sectioned, they and the adjacent septa are thickened by about 0·2 mm towards the periphery. In the counter quadrants, the septa are thin short spines as in the previous section. Measurements are difficult as the peripheral stereozone has been removed around much of these quadrants. The mean diameter is 7·5 mm and the septal formula is $C6A4K4A6C$.

In an ephebic stage section (Pl. 1, fig. 9) 14 mm higher (measured centre to centre) than the previous section, the counter quadrants are fully developed. The counter septum 1 mm thick, is thicker than all other septa, which range between 0·5–0·7 mm thick, and reaches into the axial area to meet other septal material. The flanking septa are long and pinnately arranged with their axial ends fused and coated with sclerenchyme to form strong walls parallel to the alar septa and suggesting very weak alar fossulae. The arrangement of the septa in the cardinal quadrants is similar to that described in the previous section except that the alar septa are now of similar aspect to the cardinal metasepta and meet in the axis with an angle of about 120°. The cardinal fossula is more pear shaped and the cardinal septum has shortened to 3–4 mm long (its axial end is damaged). Most of the major septa taper towards the axis but some are slightly rhopaloid and may have very thin needle-like axial extensions from the club-shaped thickening. The peripheral stereozone is 1 mm thick where it is undamaged and slight kinks in it on either side of the counter septum suggest the presence of rudimentary minor septa. The mean diameter is 14 mm and the septal formula is $C6A9K9A6C$.

A section in the ephebic stage of another specimen (R49292) shows all the septa withdrawn from the axis except the metasepta flanking the cardinal septum. These with a considerable thickening of sclerenchyme, outline an oval cardinal fossula bisected by a thin cardinal septum. The diameter is 15 mm with an estimated 38 septa ($C18K?18C$).

In longitudinal section the tabulae are largely complete with few subsidiary plates and a rather irregular spacing. They slope strongly downwards from the counter to the cardinal side with a flat or slightly undulating surface and downturned peripheral margins. Successive complete tabulae may be as much as 3–4 mm

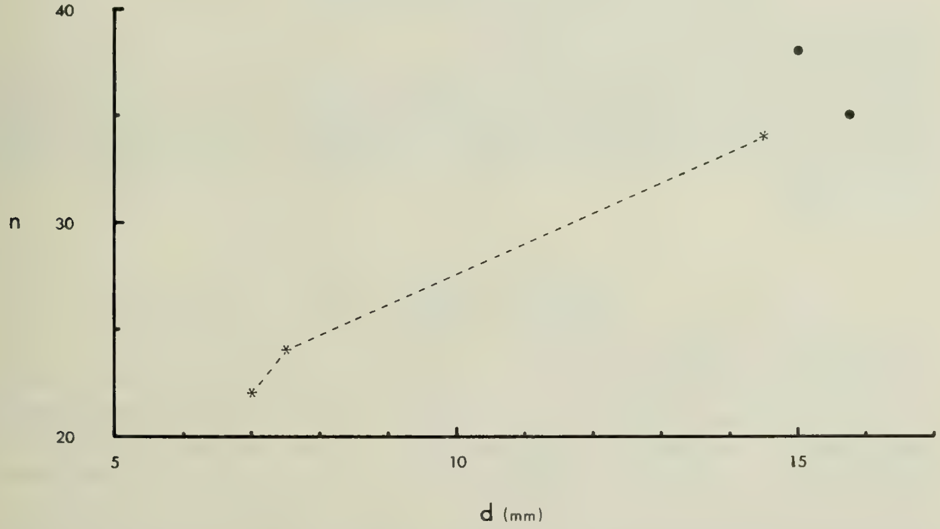

Fig. 5. Number of major septa plotted against diameter for specimens of *Amplexizaphrentis sutherlandi*. The dashed line joins asterisks representing different sections of the holotype.

apart during the late neanic-early epebic stages but become much closer-spaced, less than 1 mm at the subcalicular level. The tabulae are extensively crested with septal material in the peripheral areas. This material shows fibres directed axially and upwards at varying angles and growth lines steeply dipping at the periphery, curving round to the horizontal in the axial area. The tabulae in the axial area are coated with sclerenchyme showing a zigzag fibre pattern. Although in some places this appears to be an alteration phenomenon based on the calcite cleavage pattern, in others it appears to be original and could reflect lateral movements in the basal ectoderm of the polyp during calcification (see also Sutherland 1958 : 49). There are no dissepiments.

Discussion. This species seems to compare quite closely with *Amplexizaphrentis cassa* Sutherland (1958 : 54, pl. 8, figs 1–5, pl. 10, figs 1–4) from the middle Mississippian Kindle Formation of the Tetsa River area, and particularly closely with *A.* sp. B (Sutherland 1958 : 57, pl. 11, figs 1–5) from the Prophet Formation (?early Mississippian) of the Prophet-Muskwa Rivers area, both British Columbia. *A. sutherlandi* is distinguished by the thickness of its septa, its large size and a slightly higher septal ratio than *A. cassa.* In these features, however, it approaches very closely to *A.* sp. B of Sutherland although the cardinal fossula in the latter may be larger in proportion. The age of the Río Palmar Formation appears to be lower Pennsylvanian and thus *A. sutherlandi* is somewhat younger than either of the Canadian species.

Superfamily **ZAPHRENTICAE** Edwards & Haime 1850

Family **STREPTELASMATIDAE** Nicholson 1889

1971 *Streptelasmatidae* Scrutton: 206.

Discussion. The writer has recently outlined his views on the composition of this family (Scrutton 1971 : 206). The new genus described here stands very close to existing members of this group and does not necessitate any reconsideration of the family concept.

Genus ***BOWENELASMA*** nov.

Derivation of name. After Dr J. M. Bowen (Shell International Petroleum Corporation) who collected the material described here.

Diagnosis. Curved ceratoid corals with the cardinal septum on the convex side of the corallum. Septa dilated to close the lumen in early ontogeny; strongly dilated and more or less coated with sclerenchyme in the cardinal quadrants at the ephebic stage. Cardinal fossula narrow or poorly developed. Intertwined septal elements in the axial area may form a low boss in the calice. Minor septa well developed. Tabulae steeply sloping axially and upwards at the periphery, undulating or highly domed in the axial area. No dissepiments.

Type species. *Bowenelasma typa* sp. nov.

Discussion. *Bowenelasma* is recorded so far only from the early Middle Devonian of Venezuela. The genus is distinguished first and foremost by the strong, consistent dilatation and thickening of the cardinal quadrant septa in the later, but subcalicular, ontogenic stages. This feature appears occasionally in other streptelasmatid corals and it is also characteristic of the genus *Pseudophaulactis* Zaprudskaya in Ivanovskii (1963 : 32, pl. 6, fig. 2) from the Llandovery of the Siberian Platform. *Bowenelasma* and *Pseudophaulactis* are very similar in appearance, the latter differing only in the very attenuate nature of the septa in the counter quadrants and the general lack of twisted septal ends in the axial area (see Ivanovskii 1965, pls 5, 6 and 7, fig. 1). It should also be noted, however, that the two genera are widely separated stratigraphically and geographically.

Species of other streptelasmatid genera occasionally show significantly prolonged dilatation and thickening in the cardinal quadrants during ontogeny as a specific character or a subspecific variant. They include *Kiaerophyllum semilunatum* Scheffen (1933 : 21, pl. 2, figs 4–6) from the Upper Ordovician of the Oslo region which is considered a variant of *Grewingkia buceros* according to Neuman (1969 : 36), *Grewingkia europaeum hosholmensis* Kaljo (1961 : 58, pl. 3) from the Upper Ordovician of Estonia and the specimen identified as *Dalmanophyllum dalmani* by Ivanovskii (1963 : 36, pl. 7, fig. 4) (= *Ditoecholasma dalmani* in Ivanovskii 1965, pl. 1, fig. 6) from the Llandovery of the Siberian Platform. All these are considerably older than the new Devonian genus. *Bowenelasma* is clearly not congeneric with *Grewingkia*, which is principally distinguished by its wide spongy axial structure (Neuman 1969 : 35). *Bowenelasma* also lacks the distinctive blade-like columella so prominent in illustrations of the type species of *Dalmanophyllum* (Edwards & Haime's 1851, pl. 1, fig. 6; Minato 1961, pl. 11, figs 16, 3c, 5b).

Comparison with its contemporary streptelasmatids shows *Bowenlasma* to be readily distinguishable from all of them. This genus appears to be a late and little modified descendant of the primitive streptelasmatid structural pattern and as such contrasts quite strongly with the more structurally divergent *Heterophrentis*/*Siphonophrentis* group. *Briantelasma*, however, may be more closely related (see discussion under *Briantelasma*).

Bowenelasma typa sp. nov.

(Pl. 2, figs 1–11, Text-fig. 6)

Derivation of name. From *typus* (L.) = type, indicating the type species.

Diagnosis. *Bowenelasma* with 45 major septa at a mean subcalicular diameter of 27 mm (holotype). In ephebic stage, major septa four-fifths radius in length, dilated, coated with sclerenchyme and laterally contiguous in cardinal quadrants and slightly deflected counter-clockwise. Axial area with few septal ends intertwined to form low calicular boss. Minor septa up to one-quarter radius in length. Cardinal septum short in narrow fossula. Tabulae simple, convex, steeply sloping upwards and axially at periphery, obscured in axis but apparently gently undulating.

HOLOTYPE. R45094 (3149). Caño Grande; Caño Grande Formation, early Middle Devonian (upper Onesquethaw).

PARATYPES. R45075, R45077 (both 3121), R45100 (3157); same locality and horizon as holotype. R45121 (3618); Caño Colorado; same horizon as holotype.

OTHER MATERIAL. R45082, R49247–9, R49251 (all 3121), R49263 (3157); same locality and horizon as holotype. R45118 (3618), Caño Colorado; R45279 (3323), loose boulder on Caño del Oeste; both same horizon as holotype.

DESCRIPTION. Curved ceratoid corals up to about 90 mm long and 27 mm mean diameter at the subcalicular level. The cardinal septum is located on the convex side of the corallum. The epitheca is lightly rugate with weak septal grooves.

In the neanic stage (Pl. 2, fig. 4), the lumen is almost completely infilled by thick, irregularly pinnate septa. The major septa are between 0·6–0·7 mm thick near the periphery and taper towards the axis, contiguous with their neighbours over most of their length. Major septa in the counter and alar sectors, 3·0–3·5 mm long, reach into the axial area where they fuse and almost completely fill the lumen. The other septa wedge against these. The cardinal septum is about 1·3 mm long. Minor septa are present as very short wedges 0·7–1·0 mm long, nearly always with very small openings in the lumen beyond their axial ends. The counter septum is flanked by extra long (1·7 mm) minor septa. There are also small openings in the lumen periaxially, beyond the axial end of the cardinal septum and on the counter side of one of the alar septa. The septal formula is $C3A5K5A4C$ at a mean diameter of 7 mm.

Sections in the late neanic stage of the holotype (R45094c–d, Pl. 2, fig. 2) show major septa of very variable length twisted in a wide counter-clockwise axial vortex. Most of the major septa are 0·3–0·4 mm wide and half the radius in length. Only a few irregular septal ends cross the axial area where there may also be a few isolated spots of septal tissue. The cardinal septum is short and heavily invested with sclerenchyme. Some of the other septa in the cardinal quadrants also appear to be thickened but there is no marked contrast with the septa in the counter quadrants at this level. Minor septa cannot be easily distinguished in the wider parts of the very irregularly developed peripheral stereozone. Some of them appear to reach 2·5 mm in length and the stereozone may be up to 4 mm wide. There are 38 septa at a mean diameter of 17 mm.

In the ephebic stage (Pl. 2, fig. 1) there is a strong contrast between cardinal and counter quadrants. In both the major septa extend four-fifths of the distance to the axis and are twisted in a weak counter-clockwise vortex. Those in the cardinal quadrants however are between 1·1–1·4 mm thick and laterally contiguous for most of their length, whilst those in the counter quadrants are only 0·25–0·35 mm across and more or less parallel sided. The cardinal septum, also contiguous with its neighbours, is 5·5 mm long and situated in a weak narrow fossula closed on the axial side by a tabula and converging septa. The axial area of the coral, about a fifth of the diameter across, is traversed by two or three septal strands and traces of tabulae. There may also be a few isolated spots of septal tissue. In R45077b there is evidence that this structure in the axial area may produce a low boss in the floor of the calice. Minor septa are also well developed, as wedges of variable size up to 1·5 mm across at the base and 3·5 mm long in the cardinal quadrants and as thin spines projecting up to 2 mm beyond the peripheral stereozone in the counter quadrants. The minor septa flanking the counter septum are markedly longer than their neighbours but measurement is difficult as this part of the coral is nearly always crushed. The peripheral stereozone in the counter quadrants is quite thin, only about 1 mm thick. In the holotype, the septal formula is *C*10*A*13*K*10*A*8*C* at a mean diameter of 27 mm.

At subcalicular levels, the septa in the cardinal quadrants thin and separate from their neighbours first on the axial side of the minor septa. The cardinal septum thins most rapidly leaving a narrow, parallel sided fossula which it bisects. It maintains a length of about half the radius whilst the septa in the cardinal quadrants are still somewhat thicker than those in the counter quadrants but at slightly higher levels it rapidly withdraws to about a fifth of the radius in length. In a paratype, R45121a (Pl. 2, fig. 10), the minor septa flanking the counter septum are about 5·5 mm long at this level and the septal formula is *C*10*A*12*K*12*A*9*C* at a mean diameter of 28 mm.

The longitudinal section is dominated by septal traces and the shape of the tabulae is difficult to see. At both walls there are thick solid septal deposits, rather irregularly developed but much more pronounced on the cardinal side. In the axial area individual septal traces form a complex and irregular pattern breaking up and obscuring the tabulae. The tabulae can be clearly seen in the peripheral areas, slightly convex, moderately spaced and sloping axially and upward at 5–20° to the wall. In the axial area, the tabulae appear to be gently undulating and in one case (Pl. 2, fig. 6) sloping distinctly downward from the cardinal to the counter side. The angle of slope is difficult to assess but appears to be as much as 45° in some cases.

Measurements on the holotype and paratypes are plotted in Text-fig. 6.

Discussion. The only species so far assigned to *Bowenelasma* are the two species from the Sierra de Perijá described here. The type species, *B. typa*, which is the more abundant by a factor of three in Bowen's collection, is compared with *B. breviseptata* under the discussion of the latter species.

Bowenelasma breviseptata sp. nov.

(Pl. 3, figs 1–7; Text-fig. 6)

Derivation of name. From *brevis* (L) = short + septum, in reference to the characteristically short major septa.

Diagnosis. *Bowenelasma* with 43 major septa at a mean subcalicular diameter of 33 mm (holotype). In ephebic stage, major septa half radius in length, cardinal quadrants heavily coated with sclerenchyme peripherally. Cardinal septum very slightly longer than adjacent metasepta; no fossula developed. Wide axial area partially filled by thickened and twisted septal ends. Minor septa up to one-third radius in length. Tabulae simple, convex, steeply sloping upwards and axially at the periphery, domed in the axis or obscured by septal traces.

HOLOTYPE. R45123 (3619). Caño Colorado; Caño Grande Formation, early Middle Devonian (upper Onesquethaw).

PARATYPE. R45125 (3619). Same locality and horizon as holotype.

OTHER MATERIAL. R45105 (3199), Caño del Sur; ? R49256 (3154), Caño Grande; both same horizon as holotype.

DESCRIPTION. Large curved ceratoid corals with the cardinal septum located in the convex side of the corallum. Estimated original length of holotype 80–90 mm. The epitheca has weak septal grooves and is gently rugate.

The late neanic stages (Pl. 3, fig. 3) are largely infilled by major septa up to 1·7 mm thick and laterally contiguous along most of their length. The major septa are two-thirds the radius in length leaving a wide axial zone mostly infilled by loosely and irregularly twisted septal elements. The cardinal septum is only just over one-third the radius in length with a gap in the lumen beyond its axial end: the other protosepta cannot be distinguished. The minor septa are well developed wedges up to 5 mm long and 1 mm or a little more across the base.

In the ephebic stage (Pl. 3, fig. 1) septal thickening is confined to the cardinal quadrants. The septa are about half the radius in length with a slight anticlockwise displacement. In the cardinal quadrants the peripheral half to three-quarters of the septa are thickened to about 2 mm across bringing adjacent septa into contact.

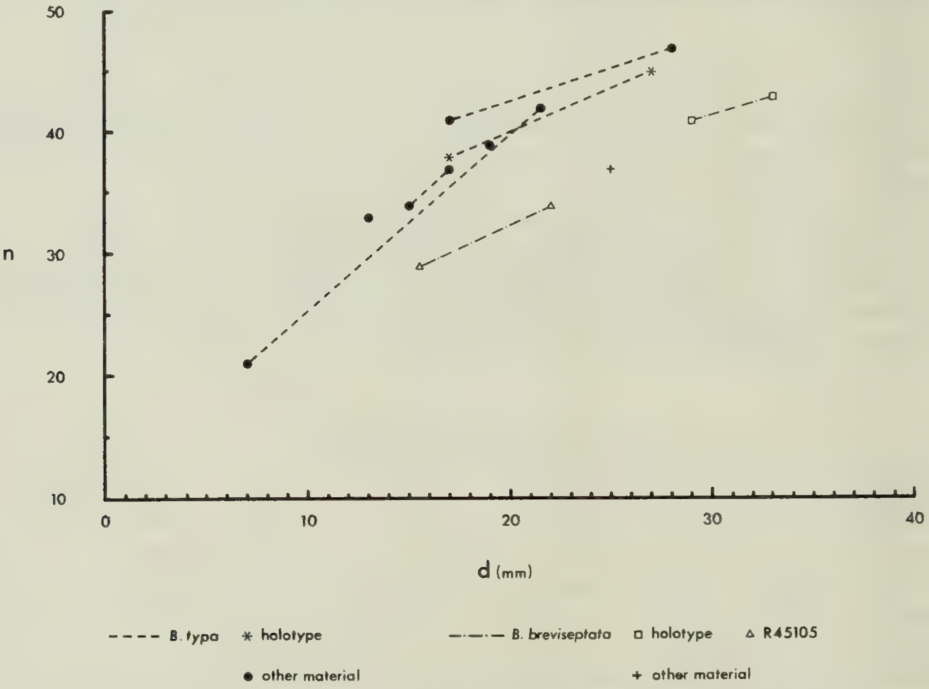

FIG. 6. Number of major septa plotted against diameter for specimens of *Bowenelasma typa* and *B. breviseptata*.

Otherwise the septa are between 0·6 and 0·7 mm across and parallel sided in both quadrants. The cardinal septum is slightly longer than adjacent metasepta with the peripheral dilatation imperfect; there is no cardinal fossula. In the axial half of the diameter, septal elements are loosely and irregularly twisted together and thickened in part. This structure forms a low boss in the floor of the calice. The minor septa are very long, and regularly developed reaching 5 mm or a third of the radius in length. Unfortunately those flanking the counter septum cannot be seen in the holotype due to crushing in this area. The minor septa are wedge-shaped in the cardinal quadrants and parallel sided to gently tapering, 0·5–1·0 mm across in the counter quadrants. The peripheral stereozone in the counter quadrants appears to be thin but is everywhere worn and cannot be measured.

R45105 (Pl. 3, figs 5–7) differs somewhat from the other specimens through its septa being generally less thickened. The section of the neanic stage available (Pl. 3, fig. 5) shows no lateral contiguity between septa. In the ephebic stage the septa are only slightly thicker in the cardinal quadrants than the counter quadrants, although the cardinal septum itself is notably thick at 1·2 mm across. The minor septa are up to 4·4 mm or two-fifths the radius in length and slightly variable in development. The septal formula is $C6A9K9A5C$ at a diameter of 22 mm.

The longitudinal section of the holotype (Pl. 3, fig. 4) is dominated by septal traces and the peripheral stereozone. The latter is particularly thick on the cardinal side. Traces of tabulae can be seen in the peripheral areas, sloping steeply axially and upwards but they cannot be identified in the axial area among the irregular vertical sections of septal elements. In R45105d (Pl. 3, fig. 7), however, the structure is very clear. The tabulae consist of large curved plates, convex upwards and outwards. They form a high axial dome and are almost vertical peripherally where they form a narrow trough against the peripheral stereozone. They are irregularly spaced between 1 and 2·5 mm vertically.

Measurements are plotted in Text-fig. 6.

Discussion. At present it is not certain how much weight should be given to the differences between R45105 and the holotype. R45105 is considered conspecific with *Bowenelasma breviseptata* here although with more material and a better understanding of the variation it may prove to be subspecifically or even specifically distinct.

B. breviseptata is distinguished from *B. typa* principally through the much shorter major septa in the mature stages and the lower septal number at comparable diameters. *B. breviseptata* also has more strongly developed minor septa and lacks any clear sign of a cardinal fossula.

Genus ***BRIANTELASMA*** Oliver 1960

1960a *Briantelasma* Oliver: 89.
1960b *Briantelasma* Oliver: 6.
1963 *Briantelasma* Oliver: 26.

Diagnosis. Trochoid to cylindrical corals with subpinnately arranged major septa extending half way or more to the axis. Lumen partly or completely infilled by laterally contiguous septa and axial sclerenchyme especially in early growth stages. Cardinal fossula present. Minor septa usually well developed. Tabulae strongly domed with axial depression, complete and closely spaced. (Based on Oliver 1960b : 6.)

Type species (by original designation). *Briantelasma americanum* Oliver 1960 : 89, pl. 14, figs 1–4. Reef facies of Coeymans Limestone, Helderbergian, Lower Devonian; Madison and Oneida Counties, New York.

Discussion. The writer follows Oliver (1960b : 6) in regarding *Briantelasma* as a member of the Streptelasmatidae in which the structural elements are completely invested in sclerenchyme during almost the full ontogeny. The ancestors of *Briantelasma* could well belong to the same lineage that evolved *Bowenelasma* as there are similarities in the basic structural patterns of the two genera. They differ principally, and very obviously, in the manner and extent of the development of sclerenchyme and also in the detailed appearance of the tabularium and the peripheral stereozone. There is no doubt that they represent distinct and divergent genera over their presently known range.

Briantelasma oliveri sp. nov

(Pl. 4, figs 1–7; Text-figs 7, 8)

Derivation of name. After Dr W. A. Oliver, Jr. (United States Geological Survey).

Diagnosis. Ceratoid to trochoid *Briantelasma* of variable size up to 39 mm diameter with 60 major septa in the holotype. Lumen completely infilled by septa and sclerenchyme to immediately sub-calicular levels. Major septa withdraw from axis to approximately half radius in length in ephebic stage. Axis plugged by structureless to vermiform loops of sclerenchyme which persists as low boss in calice. Minor septa up to one-quarter radius in length. Tabulae present in floor of calice; not distinguished in sclerenchyme.

Holotype. R45090 (3129). Caño Grande; Caño Grande Formation, early Middle Devonian (upper Onesquethaw).

Paratypes. R45091 (3129); same locality and horizon as holotype. R45119 (3618); Caño Colorado, same horizon as holotype.

Other material. ? R45099 (3157); same locality and horizon as holotype. ? R49290 (3618); Caño Colorado, same horizon as holotype. ? PRI 24426 (= 24433); ? loose block in Caño del Oeste, same horizon as holotype. ? PRI 24429 (= 24430A); same locality and horizon as holotype. ? PRI 24430B; ? locality of holotype or PRI 24426, same horizon as holotype.

Description. Ceratoid to trochoid, straight to slightly horn shaped corals up to 40 mm diameter at the base of the calice and an estimated 100 mm long. The holotype, which is the longest specimen, is incomplete and has a crushed calice. The cardinal septum is on the convex side in curved coralla. Epitheca moderately rugate and bearing weak septal grooves.

In the neanic section R45091a (Pl. 4, fig. 5) the lumen is completely or almost completely infilled by laterally contiguous septa and axial sclerenchyme. The major septa vary between half and the full radius in length and their axial ends merge into the sclerenchyme almost completely infilling the axis. They are between 0·6 and 0·7 mm in width and contiguous with their neighbours except for occasional narrow gaps between one-quarter and one-third the radius from the periphery, probably on the axial side of wedge-shaped minor septa. These minor septa are extremely difficult to distinguish but appear to be present only in the counter quadrants. There is a slight pinnate septal symmetry but again difficult to distinguish mainly due to the character of the preservation. The septal formula is *C6A8K9A6C* at a mean diameter of 10 mm.

In the ephebic stage (Pl. 4, figs 3, 6), the laterally contiguous major septa are very evenly developed 0·5 to 0·6 of the radius in length. With the exception of a few specific major septa, they all have open axial ends merging with a solid axial core of sclerenchyme which is either more or less structureless or contains a large scale vermiform pattern (R45119a, b). The septal pattern in the holotype is illustrated in Text-fig. 7. The counter septum, which is fractionally wider and longer than the average, 1·5 mm × 11 mm in the holotype, is characteristically flanked by counter-lateral septa slightly shorter than the average and with closed axial ends. Some septa in the alar areas, particularly new metasepta appearing immediately on the counter side of the alar septa are also less than average length and have closed axial ends. The cardinal septum, which is difficult to distinguish, appears to be about average length and is flanked by shorter metasepta with the next adjacent metasepta curved slightly towards the cardinal septum at their axial ends. Minor septa are well developed wedges up to a maximum of one-quarter the radius in length.

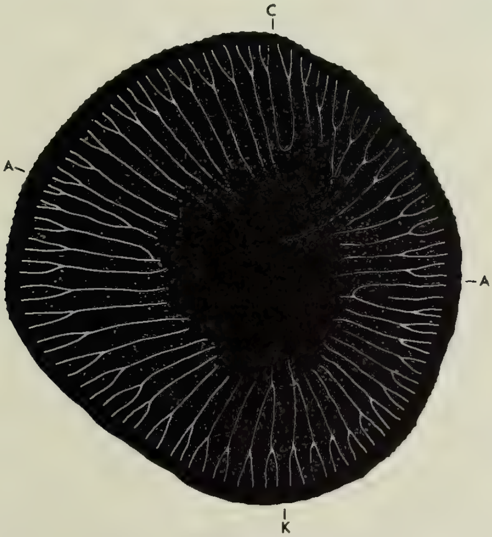

FIG. 7. Septal arrangement in *Briantelasma oliveri* (R45090a). ×2. C = cardinal septum; K = counter septum; A = alar septa.

The lumen is totally infilled. The septal formula is $C10A13K15A10C$ at a mean diameter of 23 mm in R45091b

Close to the base of the calice (Pl. 4, fig. 1) an opening first appears on the axial side of the cardinal septum which shortens rapidly at this level. A narrow elongate or sub-oval fossula is formed. Subsequently gaps appear between the major septa on the axial side of the minor septa and rapidly enlarge. The septa appear to thin almost simultaneously in all quadrants; contrasted thickening in various quadrants at this level is due to sections slightly angled to the growth lines. As the major septa withdraw to the periphery, with gently tapered axial ends, the axial plug of sclerenchyme is isolated briefly as a low mound in the calice base. At this level in the holotype, there is a peripheral stereozone 4 mm wide at a mean diameter of 39 mm. The stereozone thins in the walls of the calice and the minor septa project from it, thin and narrowly attenuate.

In longitudinal sections (Pl. 4, fig. 4), there is evidence of some gaps in between the septa and sclerenchyme at the neanic stage and in the cardinal area at later stages. Two such gaps in the cardinal area occur in the longitudinal section of the holotype (R45090e) and show signs of tabulae trough shaped against the peripheral stereozone and capped by flat subsidiary tabulae. The septa and sclerenchyme show a strongly developed grain shallowy arched across the axis and sharply down turned towards the peripheral trough-shaped tabulae. This may reflect the shape of

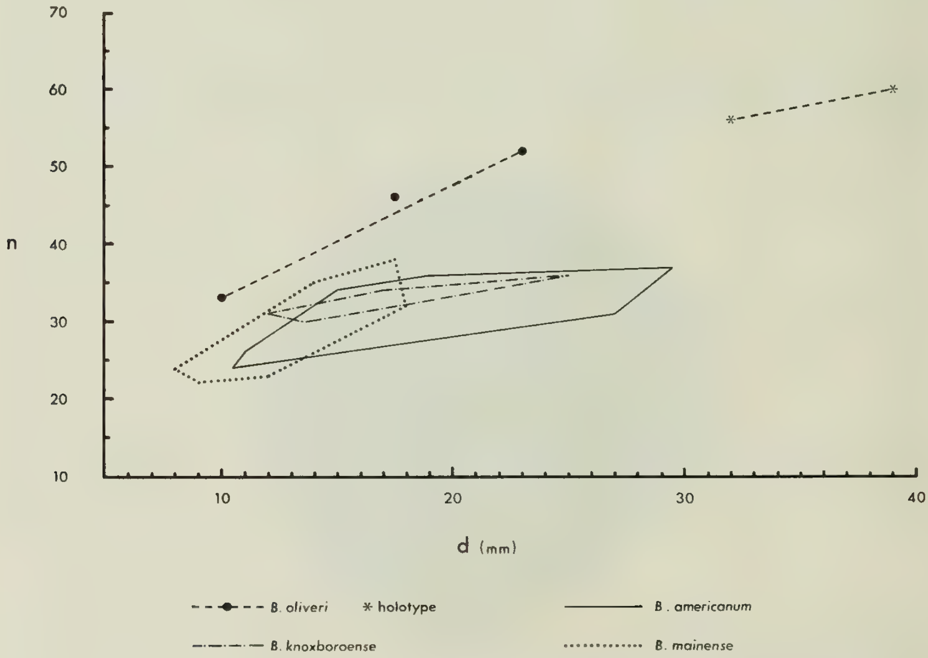

Fig. 8. Number of major septa plotted against diameter for specimens of *Briantelasma oliveri*. The polygons outline the **n**/**d** variation fields for other species of *Briantelasma*.

tabulae suppressed, or obscured in the sclerenchyme. Unfortunately no longitudinal section is available through the base of the calice, where tabulae are known to be developed, to support this.

Measurements on the holotype and paratypes are plotted in Text-fig. 8. There is a considerable variation in size, basal calice diameters ranging from 15·5 mm to 39 mm.

Discussion. Previous records of *Briantelasma* come from Silurian (? Wenlock) and Lower Devonian (Helderberg) rocks in eastern North America. *Briantelasma oliveri*, from the early Middle Devonian of the Sierra de Perijá, thus considerably extends the known range of the genus. The new species can be distinguished from all earlier described species of *Briantelasma* through the major septa withdrawing from the axis in the ephebic stage. Also, over the ontogenetic range available, *B. oliveri* lies wholly outside the fields of variation in septal number with diameter shown by the other species (see Text-fig. 8). It has higher septal ratios at corresponding diameters and reaches a higher maximum diameter than the North American species.

Genus ***HETEROPHRENTIS*** Billings 1875

Discussion. Oliver (1958 : 817, 825) suggested that *Compressiphyllum* Stumm (1949 : 13), which differs from *Heterophrentis s.s.* only through a pronounced compression of the corallum at right angles to the counter-cardinal plane, was best considered as a subgenus of *Heterophrentis*.

Subgenus ***HETEROPHRENTIS (HETEROPHRENTIS)*** Billings 1875

1875 *Heterophrentis* Billings: 235.
1938 *Heterophrentis* Stewart: 20.
1949 *Heterophrentis* Stumm: 11.
1958 *Heterophrentis* (*Heterophrentis*) Oliver: 825.
?1964 *Heterophrentis* Webby: 7.
1965 *Heterophrentis* Stumm: 18.
1968 *Heterophrentis* Altevogt: 762.

Diagnosis. Ceratoid to trochoid corals, circular in cross-section. Septa thin throughout ontogeny; major reach more or less to axis, minor up to one-third radius in ephebic stage; peripheral stereozone variable in thickness. Cardinal fossula prominent. Tabulae complete or incomplete, flat axially, arched peripherally. No dissepiments.

Type species (see Miller 1889 : 193). *Zaphrentis spatiosa* Billings 1858 : 178 = *Zaphrentis prolifica* Billings 1858 : 176 (according to O'Connell 1914 : 183). Onondaga Limestone, early Middle Devonian; Rama's Farm, near Port Colborne, Ontario, Canada.

Discussion. Numerous species of *Heterophrentis* (*H.*) have been described and the scope of the subgenus is reasonably well defined despite the fact that, according to Sutherland (1958 : 45), the original specimens of neither *Z. spatiosa*, nor *Z. prolifica* have been sectioned. The traditional interpretation of the subgenus is followed here and would surely need to be stabilised even if *Z. spatiosa* proved not to have the characters attributed to *Heterophrentis* (*H.*).

Heterophrentis (*H.*) is common in the Lower and Middle Devonian of eastern North America. The subgenus has also been recorded in the Middle Devonian of Spain and north-west Africa and is confirmed here in the early Middle Devonian of Venezuela.

Heterophrentis (Heterophrentis) venezuelensis (Weisbord 1926)

(Pl. 5, figs 1, 2)

1926 *Cyathophyllum venezuelense* Weisbord: 4 *pars.*, pl. 1, fig. 5 only.
1943 *Heterophrentis venezuelensis* (Weisbord) Wells: 97 *pars.*, pl. 10, fig. 7 only.

DIAGNOSIS. *Heterophrentis* (*H.*) with major septa two-thirds radius in ephebic stage, tapering axially; about 64 at 33 mm mean diameter in lectotype. Wide axial area occupied by tabulae only. Minor septa confined to peripheral stereozone one-quarter radius in width. Cardinal fossula present but weak. Tabulae mainly complete, gently undulating to depressed axially, sharply downturned peripherally, very close spaced beneath calice floor.

LECTOTYPE (here chosen). PRI 21594 (= PRI 24421, same specimen). Loose block (?) in Caño del Norte; Caño Grande Fm., early Middle Devonian (upper Onesquethaw).

DESCRIPTION. The lectotype is an incomplete curved conical coral 80 mm high between a diameter of 23 mm and the top of the calice. The epitheca is lightly rugate. The counter-cardinal plane is at right angles to the plane of curvature.

In the ephebic stage, 10 to 15 mm below the base of the calice, the major septa are regularly developed, 9–10 mm or two-thirds the radius in length. They are between 1 and 1·3 mm thick at the edge of the peripheral stereozone and taper gently towards the axis. Their arrangement is more or less radial except near the cardinal septum which is flanked on either side by three or four shorter metasepta and fronted axially by the concave side of a tabula. The cardinal septum itself cannot be easily distinguished but may be slightly longer than the flanking metasepta. The axial area of the corallum contains sections of tabulae but no septal material. The peripheral stereozone is between 3·5 and 4 mm wide which is also the length of the wedge shaped minor septa. There are at least 60 and an estimated 64 major septa at a mean diameter of about 33 mm and thus a septal ratio of about 1·94.

In longitudinal section, the tabulae are mainly complete and spaced about 1 mm or slightly less apart at the subcalicular level. Towards the proximal end, the spacing becomes wider and less regular. The tabulae are gently undulating or very slightly depressed across the axial area and are sharply downturned peripherally.

They appear to be inclined downwards from the convex to the concave side of the corallum. Subsidiary tabulae occur mainly on the periphery of the wide axial plateau formed by the complete tabulae. Evidence from the cross-section suggests that the tabulae are depressed in the cardinal fossula. Many tabulae have signs of septa strongly developed on their upper surfaces and some tabulae are thickly coated with septal deposits. The closer spaced tabulae in the 6–7 mm below the calice floor, however, are not affected in this way.

Discussion. The syntypes of *Cyathophyllum venezuelense* Weisbord and the additional specimens assigned to the species by Wells when he redescribed it as *Heterophrentis venezuelensis* have been re-examined with the aid of a number of new slices from which acetate peels have been prepared. No less than five species and four genera are thought to be represented. Only two of the original syntypes are species of *Heterophrentis* and these are not conspecific. One, PRI 21594 (= PRI 24421), has been selected as the lectotype and only known example of *H.* (*H.*) *venezuelensis* and is the specimen described above. The other, PRI 21593, is a specimen of *H.* (*H.*) *simplex* (Hall) and is described below. The only additional material of either species among Bowen's collection is a single specimen assigned to *H.* (*H.*) *simplex*. Of the other syntypes PRI 21592 (Weisbord 1926, pl. 1, fig. 1) is probably *Bowenelasma typa*, and PRI 21791 (Weisbord 1926, pl. 1, fig. 4) is *Heliophyllum halli*. Of the additional material studied by Wells, PRI 24426 (two thin sections cut from PRI 24433 and figured by Wells 1943, pl. 10, figs 8, 9), PRI 24429 (cut from PRI 24430A) and PRI 24430B are all questionably assigned to *Briantelasma oliveri*. Wells (1943 : 98) did observe that *Heterophrentis venezuelensis* as then understood would probably prove, with the study of additional material, to contain more than one species.

Heterophrentis (*H.*) *venezuelensis* is difficult to compare with the many species of *Heterophrentis* (*H.*) named from the Devonian of North America as very few comprehensive illustrations and descriptions for these species exist. Furthermore, the Venezuelan species is represented only by the lectotype so that its range of variation is unknown. As far as can be determined at the moment, the major septa are comparatively short in *H.* (*H.*) *venezuelensis*, with a weak cardinal fossula and minor septa confined to a well developed peripheral stereozone. This appears to distinguish the species, at least from *H.* (*H.*) *prolifica* (Billings) and *H.* (*H.*) *spissa* (Hall), the two species with which Wells (1943 : 98) chiefly compared *H.* (*H.*) *venezuelensis*. Stumm (1965 : 20) considered *H.* (*H.*) *spissa* conspecific with *H.* (*H.*) *inflata* (Hall) which he suggested in turn might be a junior synonym of *H.* (*H.*) *prolifica*. All these 'species' appear to be characteristic of the early Middle Devonian in eastern North America. *H.* (*H.*) *venezuelensis* certainly appears to differ markedly from the holotype of *H.* (*H.*) *inflata* illustrated by Stumm (1965, pl. 4, figs 11, 12). As noted above the writer believes that *H.* (*H.*) *simplex*, a third species compared with *H.* (*H.*) *venezuelensis* by Wells (1943 : 98), is actually represented by a single specimen among the syntypes. This specimen and the holotype of *H.* (*H.*) *simplex* are figured here (Pl. 5, figs 3–5) and described below. They can be seen to contrast strongly with the lectotype of *H.* (*H.*) *venezuelensis*.

Heterophrentis (Heterophrentis) simplex (Hall) 1843
(Pl. 5, figs 3–5; Text-fig. 9)

1843 *Strombodes simplex* Hall: 210, text-fig. 87, 6 on p. 209, no. 48, fig. 6 on p. 44 of tables.
1876 *Zaphrentis simplex* (Hall) Hall *pars*, pl. 21, figs 5, 8–10 (*non* figs 6, 7, 11).
1926 *Cyathophyllum venezuelense* Weisbord: 4 *pars*, pl. 1, figs 2, 3 only.
?1938 *Heterophrentis simplex* (Hall) Stewart: 23, pl. 2, figs 5–7.
1965 *Heterophrentis simplex* (Hall); Stumm: 21, ?*pars*, pl. 11, fig. 19, pl. 14, figs 5, 6.
?1968 *Heterophrentis simplex* (Hall); Stumm: 38, pl. 1, figs 6, 7.

DIAGNOSIS. Ceratoid *Heterophrentis* (*H.*). Major septa three-quarters radius in ephebic stage, thin and tapering axially with a very slight counter-clockwise deflection in axis. Cardinal septum short in suboval fossula. Minor septa one quarter radius in length, confined to or more commonly projecting from variably developed peripheral stereozone.

HOLOTYPE. NYSM 360. Middle Devonian, Hamilton Group; Moscow, New York.

OTHER MATERIAL. PRI 21593. Loose block (?) in Caño del Norte; Caño Grande Fm., early Middle Devonian (upper Onesquethaw). R49293 (3849). Caño Los Guineos; Caño Los Guineos Fm., early Middle Devonian (upper Onesquethaw).

DISTRIBUTION. Middle Devonian, Hamilton Group of New York, U.S.A. and equivalent horizons elsewhere in eastern North America; early Middle Devonian of Sierra de Perijá, Venezuela.

DESCRIPTION. The Venezuelan specimens are slightly curved incomplete ceratoid corals lacking the proximal end.

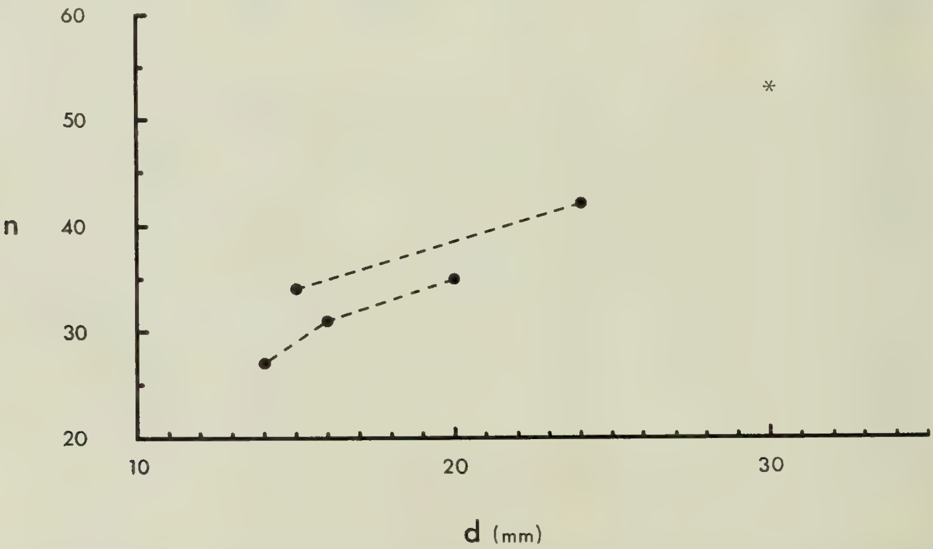

FIG. 9. Number of major septa plotted against diameter for specimens of *Heterophrentis* (*H.*) *simplex*. The holotype is indicated by an asterisk. The dashed lines join points representing different sections of the same specimen.

In the neanic stage of PRI 21593 (Pl. 5, fig. 4), the lumen is partially infilled by major septa between 0·8 and 1·0 mm thick, parallel sided and with blunt axial ends. These septa are mostly laterally contiguous along the axial third of their length where they are involved in a weak counter-clockwise vortex. A small area in the axis is free of septal material. The cardinal septum is short, 3·5 mm or half the radius in length, and flanked by short curved metasepta concave towards the cardinal septum. Towards the periphery the major septa are separated by narrow, parallel sided, ovoid or gradually widening wedge-shaped gaps terminated by the peripheral stereozone. The stereozone is rather variably developed up to 1·25 mm thick and contains traces of rudimentary wedge-shaped minor septa. The septal formula is *C7A8K8A7C* at a diameter of 15 mm.

In the ephebic stage of PRI 21593 (Pl. 5, fig. 5), the major septa are very slim and taper gently from the peripheral stereozone where they are about 0·4 mm thick to within a quarter of the radius or slightly less of the axis. There is a weak counter clockwise vortex. A few isolated bars of septal material may occur in the axis. In the cardinal quadrants, three or four metasepta flanking the cardinal septum curve to meet each other, or join sections of tabulae, across the axial end of the cardinal septum, delimiting a strong suboval fossula. The fossula is bisected by the cardinal septum, 4·5–5 mm or two-fifths the radius in length. The peripheral stereozone is variably developed from 3·3 mm thick where the minor septa are completely confined to the stereozone, to 1 mm thick from which the minor septa may project up to a further 2 mm towards the axis. There are 42 major septa at a diameter of 24 mm, a septal ratio of 1·75. Measurements are plotted in Text-fig. 9.

No longitudinal section is available.

Discussion. The Venezuelan specimens are considered conspecific with the holotype of *H.* (*H.*) *simplex* which is figured here on Pl. 5, fig. 3. The polished ephebic section of Hall's specimen is slightly larger—30 mm diameter with 53 major septa—but in other features the specimens are almost identical.

H. (*H.*) *simplex* has slimmer, longer major septa and a much more distinct cardinal fossula than *H.* (*H.*) *venezuelensis*. Furthermore, the septal ratio in this the smaller species (1·77 at 30 mm in the holotype) is lower than that in *H.* (*H.*) *venezuelensis* (1·94 at 33 mm in the lectotype).

Family **CYATHOPHYLLIDAE** Dana 1846

1963 Cyathophyllidae Birenheide: 367.
1966 Cyathophyllidae Pedder: 182, *pars*.
1969 Phillipsastraeidae Jell: 62, *pars*.

Discussion. Following his valuable revision of the Cyathophyllidae, Birenheide (1963 : 368) commented on the structural similarities between this family and the Disphyllidae, and Pedder (1966 : 182) later united the two groups of corals as subfamilies within the Cyathophyllidae. Jell (1969; see particularly pp. 64, 69), who on the other hand united the disphyllids with the phillipsastreids in the Phillipsastraeidae, has also discussed this relationship. Although disputing Pedder's classification, he did point out the close similarities of the Billingsastraeinae, a new subfamily of his Phillipsastraeidae, to the cyathophyllids.

The writer is of the opinion that *Billingsastraea* (as widely interpreted) and *Cylindrophyllum* belong together with *Heliophyllum* in the same suprageneric group. This is essentially the Billingsastraeinae of Jell (1969 : 68) with the addition of *Heliophyllum*. Birenheide (1963 : 368) included *Heliophyllum* in his undivided Cyathophyllidae but the *Heliophyllum—Billingsastraea* group, although considered here to be more closely related to the cyathophyllids than the disphyllids, deserves to be distinguished from the former on the basis of septal characteristics (see Text-fig. 11). It is therefore proposed that the Billingsastraeinae and the Cyathophyllinae be considered subfamilies of the Cyathophyllidae.

The Phillipsastraeidae is interpreted in the sense of Scrutton (1968) (= Phillipsastraeinae of Jell 1969 : 65) but admitting the Marisastrinae (*sensu* Jell 1969 : 66) if the presence of rhipidacanths can be confirmed in *Marisastrum sedgwicki*. The Disphyllidae (= Disphyllinae of Jell 1969 : 68 and ? Paradisphyllinae Jell 1969 : 67) is also accorded full family status. Perhaps the affinities of the three families Cyathophyllidae, Disphyllidae and Phillipsastraeidae would be best recognized at the superfamily level.

Subfamily **BILLINGSASTRAEINAE** Jell 1969

Genus ***HELIOPHYLLUM*** Hall 1846

1846 *Heliophyllum* Hall *in* Dana: 356.
1938 *Heliophyllum* Stewart: 35.
1938 *Heliophyllum* Fenton & Fenton: 209.
1945 *Heliophyllum* Smith: 25.
1947 *Heliophyllum* Le Maitre: 30.
1949 *Heliophyllum* Stumm: 21, *pars*.
non 1949 *Heliophyllum* Soshkina: 88.
1962 *Heliophyllum* Stumm & Tyler: 267.
1963 *Heliophyllum* Birenheide: 404.

DIAGNOSIS. Solitary or colonial rugose corals with long slender major and minor septa bearing well developed yard-arm carinae in the dissepimentarium. Septa dilated to fill the lumen in early ontogeny; dilatation may persist in tabularium of cardinal quadrants in ephebic stage. Cardinal fossula long, narrow and weak. Dissepimentarium of several rows of small globose dissepiments, horizontal or reflexed peripherally, steeply sloping downwards axially. Tabulae complete or incomplete, usually low domes but may be flat or slightly sagging.

TYPE SPECIES (by monotypy). *Strombodes helianthoides*? Hall (*non* Phillips, *nec* Goldfuss) 1843 : 209, fig. 87, 3 on p. 209, fig. 48, 3 on p. 44 of tables = *Heliophyllum halli* Edwards & Haime 1850 : 69. York, Livingstone Co., N.Y., U.S.A.; Ludlowville Fm., Middle Devonian (Hamilton Group) (Wells 1937 : 9).

DISCUSSION. Birenheide (1963) in a revision of cyathophyllids from the German Devonian has confirmed the views of Wang (1948 : 11) and others that *Keriophyllum* Wedekind is not congeneric with *Heliophyllum*. He (1963 : 392) assigned the type species of *Keriophyllum* to *Cyathophyllum* (*Peripaedium*) *turbinatum*, type species of *Peripaedium* Ehrenberg. Birenheide (1963 : 405) did regard *Keriophyllum dahlemense* Haller (1936 : 615, pl. 33, figs 1–2, pl. 34, fig. 1), however, as a valid species of *Heliophyllum*.

Heliophyllum is particularly common in the Middle Devonian of eastern North America but it has also been recorded from Europe, Asia, North Africa and South America. Some of these records may be species of *Cyathophyllum* but the acceptance of *K. dahlemense* as a species of *Heliophyllum* and the confirmation of records of *H. halli* from Spain (Altevogt 1968 : 764), North Africa (Le Maitre 1947 : 31) and Afghanistan (Brice 1971 : 263) supports this distribution in part. It is doubtful, however, if true *Heliophyllum* occurs in Australia.

Heliophyllum halli Edwards & Haime 1850

(Pl. 5, figs 6–8; Pl. 6, figs 1–6; Text-figs 10, 11)

1850 *Heliophyllum halli* Edwards & Haime: 69.
1926 *Cyathophyllum venezuelense* Weisbord: 224 (4), *pars.*, pl. 35 (1), fig. 4 only. (PRI 21791).
1937 *Heliophyllum halli* Edwards & Haime; Wells: 9, pl. 1, figs 1–15.
1943 *Heliophyllum halli* Edwards & Haime; Wells: 363 (95), pl. 36 (10), figs 1–2.
1947 *Heliophyllum halli* Edwards & Haime; Le Maitre: 31, pl. 1, figs 1–7, pl. 2, figs 1–6, pl. 3, fig. 1.
1965 *Heliophyllum halli* Edwards & Haime; Stumm: 36, pl. 32, figs 5, 6, 20–23.
1968 *Heliophyllum halli* Edwards & Haime; Altevogt: 764, pl. 2, figs 5a, b, c.
?1969 *Heliophyllum halli* Edwards & Haime; Kaplan: 28, pl. 3, fig. 1.
1970 *Heliophyllum halli* Edwards & Haime; Brice: 263, pl. 18, fig. 6.

DIAGNOSIS. Usually curved, ceratoid to turbinate solitary corals but capable of considerable shape variation and rare increase. Major septa long, uniformly attenuate in dissepimentarium but may be thickened in tabularium of cardinal quadrants. Cardinal septum slightly shorter than other metasepta in long narrow fossula, other metasepta usually arranged with bilateral symmetry about counter-cardinal plane. Minor septa one-third to one-half radius in length. Septa in dissepimentarium with well developed yard-arm carinae. Dissepiments small, globose, horizontal or inclined towards epitheca peripherally, steeply sloping towards the axis. Tabulae wide low-domed complete plates with subsidiary domed plates in axis and small, inclined subsidiary plates periaxially.

MATERIAL. R45076, R45078, R45080–1, R45084–6, R49250, R49252, R49296 (3121); R45087 (3124); R45092–3, R49253 (3145); R49254 (3149); R45096–7, R49255, R49258, R49260 (3154); R49262 (3157); all Caño Grande; Caño Grande Formation. R45104, R49268–9 (3199); R45107–9, R49274 (3221); all Caño del Sur; Caño Grande Formation. R45120, R45122, R49286, R49288–9 (3618); R45124

(3619); all Caño Colorado; Caño Grande Formation. R45111–5, R49277–8, R49281, R49284 (3323); all from loose boulder in Caño del Oeste; Caño Grande Formation. R45128, R49294–5 (3849); all Caño Los Guineos; Caño Los Guineos Formation. All early Middle Devonian (upper Onesquethaw).

Distribution. Widespread in Middle Devonian of eastern North America and also present in the Middle Devonian of North Africa, Spain, Afghanistan and Venezuela. Records of this species from other areas doubtful.

Description. Curved conical trochoid to turbinate corals attaining a maximum mean diameter of 38 mm and a height of about 50 mm. Corallum shape not greatly variable. Epitheca with very weak septal grooves and gently rugate. The cardinal fossula is invariably located on the convex side of the corallum.

In neanic sections, the lumen is almost entirely closed by thickened septa. In R45104c (Pl. 6, fig. 2), the major septa, 0·8–1·1 mm thick extend almost to the axis where their ends are coated with sclerenchyme which fills the axial area. Along their length they are laterally contiguous in parts and separated elsewhere by a narrow sub-parallel sided gap between 0·05 mm and 0·2 mm wide crossed at intervals by the traces of tabulae. There is a distinct bilateral symmetry, the cardinal septum being longer than all the other septa and flanked by pinnate groups of metasepta. Minor septa appear mostly as short wedges up to 2·8 mm long and 0·7 mm wide between the peripheral ends of the major septa forming a solid septal stereozone around the cardinal quadrants. In the counter qudrants, however, there is a very narrow unthickened zone around the periphery, about half as wide as the length of the minor septa, in which major and minor septa alike are 0·2–0·3 mm wide. Signs of carinae are seen only rarely as incipient structures within the thickened peripheral parts of some septa. R45104c is 14·5 mm in mean diameter with 35 major septa.

In higher sections (R45108a, R45111c), the unthickened peripheral zone in the counter quadrants grows in width and gradually extends circumferentially across the alar areas towards the cardinal septum. Yard-arm carinae appear, one or two per septum, on the peripheral unthickened parts of the septa. In the axis, where there may be a weak counter-clockwise vortex, the core of sclerenchyme disappears in most cases and the ends of the septa, usually just short of the centre, may be gently tapered in an axial zone about 0·2 of the diameter across. The cardinal septum shortens and the arrangement of the flanking metasepta defines a long narrow cardinal fossula, well developed in some sections but hardly distinguishable in others.

Septal thickening is developed on the crests of the innermost series of dissepiments and the tabulae. It begins to diminish first in the counter quadrants and often disappears here completely by the late neanic—early ephebic stage. The boundary between the unthickened and thickened portions of the septa remains sharp until all trace of thickening disappears. The cardinal quadrants, however, are usually heavily thickened into and throughout much of the ephebic stage, often with the septa laterally contiguous except in the long narrow cardinal fossula. The outer edge of the thickened zone moves inwards towards and usually across the dissepimentarium/tabularium boundary, and the zone itself may be as small as half the diameter in width in some ephebic sections. On the cardinal septum and one or two flanking metasepta, however, the thickening starts very much closer to the periphery and serves to emphasise the cardinal fossula.

In ephebic sections the epitheca is about 0·25 mm thick and the peripheral parts of the septa about 0·1 mm across. The major septa, with the exception of the cardinal septum and a few flanking metasepta, all reach the axial area usually with tapered ends bilaterally arranged about the counter-cardinal axis. Nearly always the major septa are slightly thickened in the inner part of the tabularium. Sections such as R49278a (Pl. 6, fig. 5) with no notable septal thickening at all are rare. One specimen R45115a–b (Pl. 5, fig. 6) shows an irregular network of septal material in an axial area about a fifth the diameter across. Minor septa range from a third to just over half the radius in length and those flanking the counter septum may be slightly longer than their neighbours. Yard-arm carinae are developed on major and minor septa in the dissepimentarium, rarely with a strong contrast between counter (better developed) and cardinal quadrants. Variation from specimen to specimen is notable with individual carinae between 0·4 and 0·65 mm in average width, 0·6 to 1·2 mm in average spacing and between means of 3 to 6 per septum. The intensity of carination tends to increase with increasing size and septal number and with decreasing septal thickening. The appearance of the cardinal fossula is also variable with the cardinal septum ranging between extremes of a quarter to two-thirds of the radius in length in a narrow, parallel sided fossula closed axially by the incurving ends of the adjacent metasepta. Dissepiments are intercepted on average 0·5 mm apart, usually uniserial between adjacent septa. Up to three rows closest to the epitheca are concave abaxially, the rest concave adaxially. They may in some cases loop between carinae rather than from septum to septum. Traces of tabulae are wider spaced and more diffuse.

In longitudinal section, the lower parts and much of the peripheral areas particularly on the cardinal side are infilled by sclerenchyme. The dissepimentarium is composed of small globose dissepiments up to 1·2 mm high but normally fairly evenly developed around 0·75 mm high. The width of the dissepimentarium increases towards the calice and contains up to six rows of dissepiments. They are horizontal to slightly reflexed peripherally and steeply sloping downwards axially. The dissepimentarium is notably modified in the cardinal fossula (Pl. 6, fig. 6) where the peripheral two or three rows of normal globose dissepiments are followed axially after a sharp break by large axially and downward sloping vesicles. The tabulae are complete and incomplete. The complete series are broad low domes 1–2 mm apart. The incomplete tabulae are mainly subsidiary broad low domes across the axial four-fifths of the tabularium diameter with a few small flanking vesicles. The sclerenchyme coating the septa is commonly seen cresting the tabulae as well. Traces of carinae are confined to the dissepimentarium. Close to the epitheca they slope inwards and upwards at no more than 10° to the wall, but towards the axis they curve over to an angle of about 45° and occasionally as low as 30° to the horizontal.

Septal microstructure is only clear in parts, where uniserial monacanthine trabeculae can be seen. The cross-bar carinae which cut, and definitely precede the septa in formation have the same general appearance as septal tissue but no details of their trabecular structure can be determined.

Measurements of septal number against diameter are plotted in Text-fig. 10.

Discussion. Although the Venezuelan specimens have a considerably smaller range of adult diameters than topotypic *Heliophyllum halli* (see Text-fig. 10) there appears to be no structural distinction of note between the two groups of specimens. Size and size linked factors such as septal number and intensity of carination, and possibly also the more prevalent septal thickening in the Venezuelan sample are probably all of ecological rather than genetic importance. Furthermore, although the legendary variability of *H. halli* in external form is well documented (Wells 1937), variation in internal structure is not so well known neither for this species nor for the host of other North American 'species' of *Heliophyllum* (see for example Stumm (1965 : 35–38)). For these reasons it seems preferable not to distinguish the Venezuelan material in any way from *H. halli*.

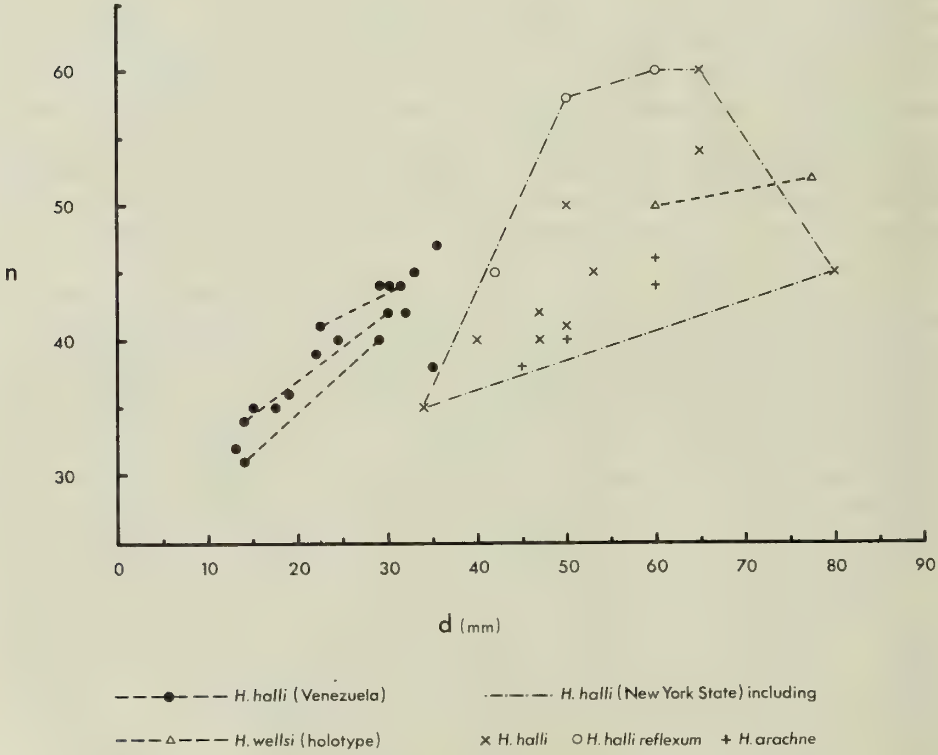

Fig. 10. Number of major septa plotted against diameter for specimens of *Heliophyllum halli* from Venezuela and New York State, and for specimens of *H. wellsi*.

Heliophyllum wellsi sp. nov.

(Pl 6, figs 7, 8; Pl. 7, figs 1, 2; Text-figs 10, 11)

DERIVATION OF NAME. After Professor J. W. Wells (Cornell University, Ithaca, N.Y., U.S.A.).

DIAGNOSIS. Large solitary *Heliophyllum* with dissepimentarium one-half to three-fifths the radius. Attenuate major and minor septa densely carinate in dissepimentarium. Carinae yard-arm, sometimes with branching ends; they may form reticulate network with septa close to the epitheca. Axial core of reticulate septal lamellae about one-fifth the diameter across. Dissepiments small, globose, numerous; tabulae incomplete, tabularium horizontal or slightly domed.

HOLOTYPE. R45088 (3126). Caño Grande; Caño Grande Formation, early Middle Devonian (upper Onesquethaw).

PARATYPE. R45089 (3126). Same locality and horizon as holotype.

DESCRIPTION. The specimens are large conico-cylindrical fragments of the mature stages of two coralla. The epitheca is moderately rugate.

In cross-section the epitheca is 0·2 mm thick and only slightly penetrated by the expanded and shallowly convex ends of the septa. The septa are extremely thin across the broad dissepimentarium, measuring 0·05–0·10 mm across; the peripheral expansion is variable but not more than 0·30 mm across and less than 1 mm long. There is no sign of a cardinal fossula. In the dissepimentarium, the septa bear abundant yard-arm carinae, averaging 22–24 per septum, spaced 0·7 mm apart and reaching 2 mm in length near the periphery. The carinae towards the inner dissepimentarium are shorter and closer spaced normal cross-bars but many of those in the outer dissepimentarium have bifurcating or geniculate ends. In some instances septa and carinae may form an intricate reticulate network just inside the epitheca. The minor septa are about as long as the dissepimentarium is wide, that is half to three-fifths the radius. A slight but well defined septal thickening to 0·3–0·4 mm in width takes place at the dissepimentarium-tabularium boundary, gently tapering towards the axis over some 5–7 mm. Incipient carinae can be clearly seen embedded in these thickened parts of the major septa in higher ephebic sections. The axial ends of the major septa terminate against an axial area 10–20 mm across containing a dense and rather irregular reticulate network of septal material which is occasionally weakly carinate. The details of this axial structure show considerable variation in the sections available.

In longitudinal section the dissepimentarium is composed of numerous small globose dissepiments on average 0·7 mm high, horizontally arranged near the periphery and curving over to slope steeply downward towards the axis. The tabulae are incomplete longer, flatter, vesicular plates arranged horizontally or slightly domed across the axis. In the axial three-fifths of the tabularium diameter, the tabulae are disrupted by numerous, vertical and sub-parallel, wavy septal lamellae. The dissepimentarium is crossed by the traces of carinae, very regularly spaced 0·5–0·6 mm apart normal to their length. The carinae are inclined 25–30° to the epitheca at the periphery, curving over gently through 40° to lie approximately

40° to the horizontal at the inner edge of the dissepimentarium. They may just penetrate the tabularium, bending sharply upwards through about 20° as they do so.

Diameter and septal number in the holotype are plotted on Text-fig. 10. The paratype, of comparable size, is too crushed to measure accurately.

The fine structure of the epitheca, dissepiments and tabulae can be clearly seen to be fibronormal. The septa appear to be composed of unitrabecular monacanths and the fine structure of the carinae is of septal type but is otherwise obscure.

Discussion. *Heliophyllum wellsi* is distinguished in general by its large size, the intensity of the septal carination and the apparent lack of a cardinal fossula. The most striking feature of the new species, is however, the axial core of reticulate septal lamellae which appears to be unique to *H. wellsi* among species of *Heliophyllum.*

Genus ***CYLINDROPHYLLUM*** Simpson 1900

1938 *Cylindrophyllum* Stewart: 43.
1949 *Cylindrophyllum* Stumm: 33.
1949 *Cylindrophyllum* Ehlers & Stumm: 23.

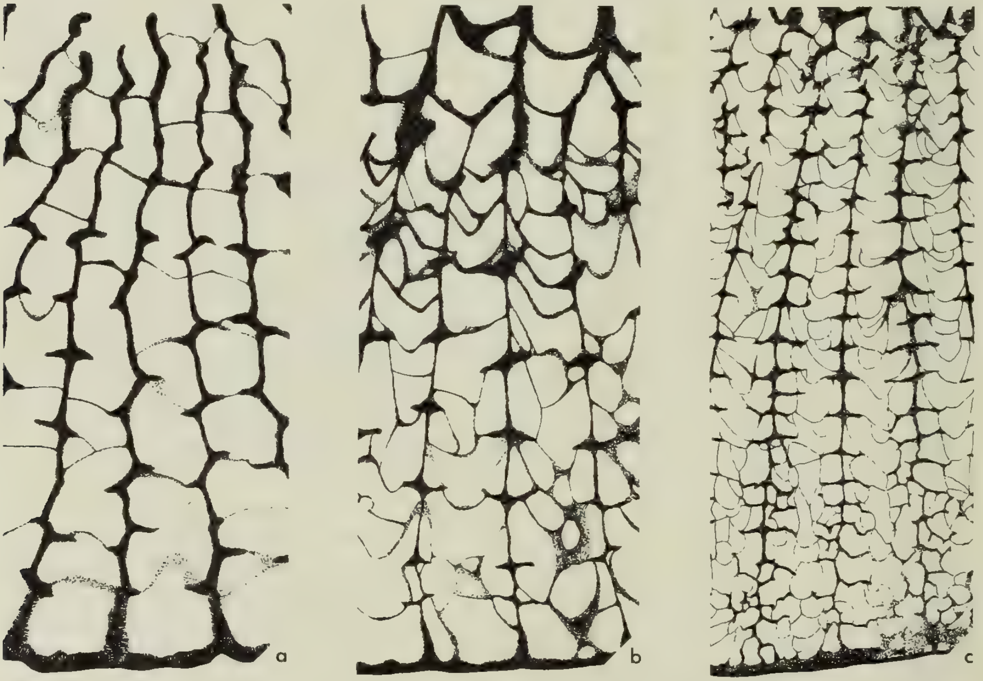

Fig. 11. Comparative septal carination in (a) *Cylindrophyllum elongatum* (R45116a) ×25, (b) *Heliophyllum halli* (R45115a) ×10, and (c) *Heliophyllum wellsi* (R45088a) ×6.

DIAGNOSIS. Dendroid or phaceloid rugose corals. Corallites with attenuate major and minor septa and radial symmetry. Septa with variably developed yard-arm carinae in dissepimentarium, the major septa irregular in course with occasional lateral projections in tabularium and frequently withdrawn from axis. Dissepiments small, globose, usually sloping steeply downwards towards the axis. Tabulae mainly incomplete; tabularium surface usually bowl-shaped, occasionally flat or more rarely arched.

TYPE SPECIES (by original designation). *Cylindrophyllum elongatum* Simpson 1900 : 217, text-fig. 42. Onondaga Limestone (Edgecliff Member), early Middle Devonian; Clarksville, Albany Co., N.Y., U.S.A.

DISCUSSION. *Cylindrophyllum* has been commonly placed in the Disphyllidae but the septal characteristics in particular suggest that the genus is more likely to be related to the *Heliophyllum-Billingsastraea* group (see discussion of the Cyathophyllidae).

Cylindrophyllum elongatum Simpson 1900

(Pl. 7, figs 3–6; Text-fig. 11)

1900 *Cylindrophyllum elongatum* Simpson: 217, fig. 42.

DIAGNOSIS. Phaceloid *Cylindrophyllum* with corallites up to about 20 mm diameter. Major and minor septa almost equal in length, more or less confined to dissepimentarium. Septa straight or zigzagged, carinae usually well developed but may be variable to almost absent in some corallites. Dissepiments small, globose, up to four rows deep, strongly sloping axially and downwards. Tabulae complete or incomplete; tabularium surface flat or bowl-shaped, rarely arched.

MATERIAL. R45116 (3539). Slipped block in Caño Pescado; Caño Grande Formation or lower part of Caño del Oeste Formation, early Middle Devonian (upper Onesquethaw).

DISTRIBUTION. Onondaga Limestone; New York, U.S.A. Caño Grande Fm. or lower Caño del Oeste Fm. Sierra de Perijá, Venezuela. Both early Middle Devonian.

DESCRIPTION. The specimen is a portion, 120 mm × 100 mm × 70 mm, of a phaceloid colony in which most of the corallites are partially crushed. There are no signs of connecting processes between corallites in this colony.

In cross-section the corallites were nearly all originally circular with a regularly developed fibronormal epitheca 0·1 mm thick. In a few cases, adjacent corallites grow with short lengths of their epithecae cemented back to back. Major and minor septa are uniformly attenuate, 0·03 mm thick on average, except in the peripheral 1 mm or less in which they gradually thicken towards the epitheca. The septa have very bluntly wedge-shaped peripheral ends reaching 0·25 mm in thickness which may penetrate up to half the thickness of the epitheca. Major and minor septa appear to be formed of unitrabecular monacanthine trabeculae and are differentiated by no more than 0·3 to 0·4 mm in length. They reach between a half and two-thirds the radius to the axis, the minor septa ending at the tabularium/dissepimentarium boundary, the major septa just penetrating the tabularium. The septa may be straight or zigzagged. A few corallites have scattered carinae on one or two septa only but most corallites have moderately developed carinae on all or nearly all septa. The carinae appear to be of the yard-arm type as developed in *Heliophyllum* but many are geniculate with a central portion displacing the septum obliquely and only the extremities orientated normal to the septal face, thus giving the appearance of alternate carinae on zig-zag septa. Dissepiments usually appear as a single series between septa of straight to slightly curved bars 0·3–0·5 mm apart. There is a wide axial area between a third and a half the radius across free of septa and crossed only by curved sections of tabulae. No signs of the type of increase were observed. Because of the crushing, accurate measurements were possible on only a few corallites. The largest individual was 10·5 mm in diameter with 29 major septa.

In longitudinal section the dissepiments are small, globose and regularly developed 0·4–0·6 mm high. The dissepimentarium is usually four rows, or sometimes possibly five rows of dissepiments deep. The surface slopes axially and downwards at 45°–55° to the horizontal. The carinae crossing the dissepimentarium may be almost parallel to the epitheca at the periphery but incline more and more towards the axis when traced towards the inner edge of the dissepimentarium where they are 45°–50° to the horizontal. The tabulae are complete and incomplete, arranged horizontally or with a slight axial depression. The complete tabulae are either slightly arched or more usually slightly sagging and are supplemented or partially replaced by large vesicular plates.

Discussion. This specimen appears to be conspecific with photographs of the holotype and other specimens from the Edgecliff member of the Onondaga Limestone of New York kindly provided by Dr W. A. Oliver, Jr. (U.S. Geological Survey). The only points of difference appear to be a tendency for the New York material to have a higher percentage of complete tabulae and to reach a larger corallite diameter.

The diagnosis for the species given here has been constructed with the aid of these photographs.

Family **DURHAMINIDAE** Minato & Kato 1965b

1965b Durhaminidae Minato & Kato: 28.
1967 Durhaminidae Stephens: 426.
1967 Durhaminidae Federowski: 25.

Diagnosis. Solitary, fasciculate, cerioid or plocoid rugose corals. Axial structure with median counter-cardinal plate in early ontogeny, poorly developed or lost in ephebic stage and replaced by few irregularly arranged septal ends or septal lamellae. Minor septa variably developed and scattered third order septa may occur. Septa usually thin, sinuous or zigzagged in dissepimentarium, slightly dilated in tabularium. Lonsdaleoid dissepiments may be variably developed, the others concentric or herringbone: all dip steeply axially and downwards. Tabulae mainly incomplete, peripherally flat or trough-shaped, axially flat-topped or arched domes. Clinotabellae usually present. Axial tabellae may or may not be clearly differentiated.

Type genus. *Durhamina* Wilson & Langenheim 1962 : 504.

Discussion. The specimen described below as *Durhamina* sp. nov. definitely possesses poorly developed sporadic third order septa and an examination of Easton's (1960, text-fig. 18) illustration of the holotype of *Lonsdaleia cordillerensis* (lower right quadrant of largest corallite) shows them to be present to a similar extent in the type species of *Durhamina* itself. This serves to underline the extremely close relationship between the Durhaminidae and Waagenophyllidae and is of particular interest in view of Minato & Kato's (1965a : 13) observations on tertiary and higher orders of septa in the Waagenophyllidae. The diagnosis given above is emended accordingly.

Members of the Durhaminidae occur in the Middle Carboniferous to Middle Permian rocks of Eurasia, western North America and South America.

Genus ***DURHAMINA*** Wilson & Langenheim 1962

1962 *Durhamina* Wilson & Langenheim: 504.
1965b *Durhamina* Minato & Kato: 34.

Diagnosis. Fasciculate Durhaminidae with weakly constructed axial structure and scattered, weakly developed third order septa. Lonsdaleoid dissepiments sporadically developed.

Type species (by original designation). *Lonsdaleia cordillerensis* Easton 1960 : 580, Text-figs 17, 18. Lr. Permian; nr. Ruth, eastern Nevada, and other localities in eastern Nevada and southern California, U.S.A.

Discussion. Wilson & Langenheim (1962 : 504) provided a very full comparison of *Durhamina* with similar genera, supplemented by Minato & Kato (1965b : 34). It is only necessary here to draw attention to the scattered third order septa (see discussion of family) not hitherto recorded in the genus.

?***Durhamina*** sp.

(Pl. 7, figs 7, 8)

Material. R49285 (3495). Caño del Norte; Río Palmar Formation, Lr. Pennsylvanian.

Description. Solitary cylindrical fragment 9 mm maximum diameter.

In cross-section the epitheca is thin and smooth. The major septa are between a half and the full radius in length and are very slightly thicker in the tabularium than dissepimentarium. The longer septa meet in the axial area, the shorter septa have free tapered ends. Minor septa are fairly evenly developed, up to a third the radius in length. Dissepiments are concentric between them and their flanking majors but weakly herringbone beyond their axial ends when they are particularly short. There are no lonsdaleoid dissepiments. There are 21 major septa at a diameter of 7·5 mm.

In longitudinal section the dissepimentarium is narrow, a quarter the radius in width, and composed of steeply inclined vesicles averaging 1 mm long and 0·25–0·3 mm high. The tabulae are complete and incomplete but mostly the latter. The complete tabulae are flat or gently sagging across the axis and downturned peripherally. The incomplete tabulae are undulating plates, inclined gently axially and upwards to meet the vertical trace of a septum in the axis. There are scattered clinotabellae.

DISCUSSION. This fragment can be closely matched with corallites from species of *Durhamina* in which the axial structure is weak, and is therefore assumed to be part of a corallite detached from a fasciculate coral colony. In view of the limitations of the single specimen, however, the identification must be treated with reserve.

Durhamina sp. nov.

(Pl. 8, figs 1–10; Text-fig. 12)

MATERIAL. R49276 (3270). From a boulder in the Caño Grande; horizon uncertain, ? Río Palmar Fm., Lr. Pennsylvanian, but see p. 232.

DESCRIPTION. The specimen is a large fragment, some 150 × 150 × 100 mm before cutting, of a phaceloid or in parts cerioid colony set in a tough fine-grained reddish-brown calcareous matrix. No external details of the corallites can be observed.

In cross-section, the corallites are circular when free and uncrushed. There are areas in the colony where groups of three to eight corallites become laterally contiguous and assume a cerioid habit. Young hysterocorallites have slim major septa, three-fifths to the full radius in length from corallite to corallite but of fairly uniform length within a single corallite. In the smallest corallite (Pl. 8, fig. 5), 4 mm in diameter, the major septa are about 0·07 mm thick near the periphery, tapering towards but not reaching the axis. The counter septum, however, crosses the axial area with a slim blade-like expansion centred on the axis, 0·8 mm long and 0·12 mm thick, which imparts a strong bilateral symmetry to the corallite. In slightly larger corallites (Pl. 8, figs 6, 7) with longer major septa, several of them meet in the axis often deflecting the end of the counter septum or obscuring its identification and the bilateral symmetry is weakened or lost. The peripheral ends of the septa are often, but not in all corallites, interrupted by a single series of lonsdaleoid dissepiments. When the septa are not interrupted they are usually somewhat irregular in course and thickness at the periphery. The dissepiments are very variable in appearance. Among the lonsdaleoid series and the inner two or three series of similar sized normal dissepiments are scattered very much smaller and more highly globose dissepiments. The dissepiments are irregularly arranged in a single series or weakly herringbone between adjacent major septa. Minor septa are absent or sporadically developed as short spines on the dissepiments.

In mature corallites, most major septa extend from the epitheca to the axis with occasional interruptions along their length. The epitheca is a very smoothly and regularly developed fibronormal wall 0·12 mm thick. It shows no signs of septal grooves. The septa which have slightly expanded, flat to shallowly convex or wedge shaped peripheral ends show little or no penetration of the inner face of the epitheca. The major septa are slim and are usually irregularly zigzagged or sinuous in the dissepimentarium due to dissepimental interference. They are not frequently interrupted, however, and there is no well defined series of lonsdaleoid dissepiments. Most septa show a slight and often sharp dilatation at the inner edge of the dissepimentarium associated with a slight thickening of the innermost series of dissepiments. Major septa are between 0·1 and 0·2 mm thick at this point from which they taper smoothly towards the axis. In any one corallite about half the major septa will meet in the axis usually resting against an irregular median plate formed by the extended end of what is assumed to be the counter septum. These septa may be slightly thickened in the immediate axial area. The rest of the major septa taper to a point just short of the axis. A few of the septa may be interrupted periaxially thus lending definition to the axial structure but no additional septal lamellae are involved. Also, tabulae are intercepted more frequently in the axial area. Minor septa are extremely irregularly developed. In some corallites they extend to or just across the dissepimentarium/tabularium boundary, or very rarely up to half way across the tabularium to the axis. They are very thin and zigzagged in the dissepimentarium or may be frequently interrupted. At the other extreme the minor septa may be no more than scattered spines on the crests of a few dissepiments. The dissepimentarium is between 0·3–0·4 of the radius in width and disordered in appearance. An irregular herringbone pattern is developed either between major septa when the minor septa are weak, or between major and minor septa when the minor septa are strong. In the latter case, scattered third order septa are developed as very short pegs on the epitheca and as short spines cresting dissepiments (Pl. 8, fig. 2). Septal structure, although clearly trabecular, cannot be distinguished in detail and the style of increase cannot be determined in cross-section.

In longitudinal section the dissepiments are mixed larger, less inflated, rather elongate vesicles and smaller, more globose vesicles. The longer vesicles may reach up to 3–4 mm long and 1 mm high normal to the dissepimental surface, whilst the smaller average about 0·75 mm long and 0·4 mm high. The dissepiments slope steeply and fairly uniformly axially and downwards at about 50° to the horizontal. The tabularium is wide, between 0·6 and 0·7 of the diameter and consists of complete and incomplete plates. Complete tabulae are rare, fairly wide flat-topped domes with the peripheral extremities sigmoidally curved downwards and meeting the dissepimental wall horizontally. The incomplete tabulae are axially dome-shaped and periaxially trough-shaped plates with occasional clinotabellae, combined to give a broad axial plateau to the tabularium surface, which may be gently domed or depressed across the axis. There is no sign of any great modification of the tabulae in the axial area corresponding to the weak axial structure in cross-section. In longitudinal section, increase appears to be peripheral non-parricidal or lateral.

Measurements of corallite diameter and septal number are plotted in Text-fig. 12. Corallites reach a maximum of 18 mm diameter but data are restricted by the partial crushing of many corallites.

Discussion. *Durhamina* sp. nov. compares most closely with *D. cordillerensis* (Easton) from the Lr. Permian of Nevada and California although it can be distinguished from that species on a number of points. The most striking is the more regular development and greater simplicity of the axial structure in the Venezuelan species. In *D. cordillerensis* the axial structure is of quite variable density and may rarely be absent. When it is well developed, however, the septal lamellae involved are clearly distinguished from the major septa, in contrast to the very primitive arrangement in *Durhamina* sp. nov. The latter also has a more strongly developed dissepimentarium than *D. cordillerensis* and indeed most other species of *Durhamina*. Finally the Venezuelan species has larger corallites than the North American species. Mature corallites are about 14 mm mean diameter with 22–25 major septa, reaching a maximum of 18 mm diameter in *D.* sp. nov., compared to mean diameter about 8–9 mm with 22 to 28 major septa (Easton 1960 : 580) or 20–22 major septa (Wilson & Langenheim 1962 : 506) and maximum diameter about 15 mm in *D. cordillerensis*.

The Venezuelan species has not been formally named here as it is represented by only a single specimen from a loose block of uncertain stratigraphic position.

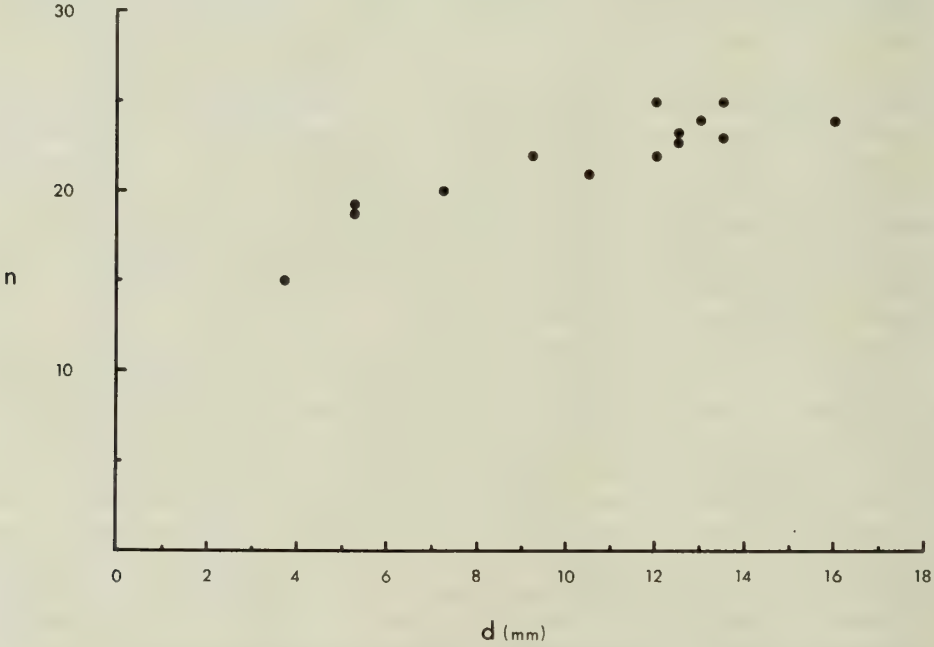

Fig. 12. Number of major septa plotted against diameter for corallites in one colony of *Durhamina* sp. nov.

Suborder CYSTIPHYLLINA Nicholson 1889
Family **CYSTIPHYLLIDAE** Edwards & Haime 1850
Subfamily **PLASMOPHYLLINAE** Dybowski 1873

1964 Plasmophyllinae; Birenheide : 15.

Genus ***PLASMOPHYLLUM*** Dybowski 1873

1873 *Plasmophyllum* Dybowski : 340
1964 *Plasmophyllum* (*Plasmophyllum*); Birenheide: 16 *cum syn.*

Diagnosis. Solitary or weakly colonial corals in which the lumen is filled by vesicular tissue which may or may not be thickened with sclerenchyme. Septa are absent or represented by short irregularly developed spines. The vesicles in general increase in size towards the axis and are arranged with a shallow bowl-shaped to inverted sub-conical surface. Thickening when present is based on this surface and may extend from epitheca to axis or be confined to a single concentric zone.

Type species (by subsequent designation of Schlüter 1885 : 10). *Cyathophyllum limbatum* Quenstedt 1879 : 465, pl. 158, fig. 37 (*non* fig. 38) = *Cyathophyllum goldfussi* Edwards & Haime 1851 (*non* Castelnau 1843). Gerolstein, Eifel, Germany; Ahrdorf-Schichten, Middle Devonian (Eifelian).

Discussion. Birenheide (1964) has provided a most valuable review of the Devonian cystimorph group of corals, placing them all, with a few exceptions, in the subgenera *Plasmophyllum* (*Plasmophyllum*) and *Plasmophyllum* (*Mesophyllum*). The writer feels, however, that these two groups deserve full generic status based on the distinction in septal development between them and that their close relationship is best indicated at the subfamily level.

Plasmophyllum secundum americanum (Edwards & Haime) 1851
(Pl. 9, figs 1–4)

1851 *Cystiphyllum americanum* Edwards & Haime: 464, pl. 13, figs 4, 4a.
1964 *Plasmophyllum* (*Plasmophyllum*) *secundum americanum* (Edwards & Haime) Birenheide: 23, pl. 24, fig. 117 (*cum syn.*).

Diagnosis. Trochoid or turbinate tending to subcylindrical *Plasmophyllum* with vesicles clearly separable into two concentric zones. Vesicles of the inner zone slightly larger than in the outer zone and increasing in size towards the axis in both zones. Short blunt septal spines developed, particularly in the inner half of the outer zone. Usually sclerenchyme is heaviest in a broad concentric band or bands coating or completely obscuring the vesicles in the outer part of the inner zone.

Material. R45098 (3157). Caño Grande; Caño Grande Formation, early Middle Devonian (Upper Onesquethaw). R45106, R49270, R49272 (3221). Caño del Sur; Caño Grande Formation, early Middle Devonian (upper Onesquethaw).

Distribution. Widespread in rocks of Middle Devonian age in North America. Caño Grande Fm., early Middle Devonian; Sierra de Perijá, Venezuela. Also present in the Middle Devonian of Spain, U.S.S.R., south-east Asia and Australia according to Birenheide (1964 : 24, synonymy).

Description. Turbinate corals up to 40 mm diameter and 70 mm height. Calice a shallow bowl with a strongly everted rim. Epitheca moderately rugate.

In cross-section, the epitheca is fibronormal and of somewhat variable thickness, 0·1–0·3 mm thick in the small part preserved. The lumen is entirely filled by vesicular tissue, fine in an outer zone one-third the radius across in smaller sections to one-half the radius in the largest subcalicular section, and coarser in the axial zone. In the peripheral area the vesicles are highly globose and often circular or subcircular in cross-section, but somewhat variable in shape and generally ranging in diameter from 0·5 to 2 mm. They may be thin walled or lightly coated with fibronormal material locally extended into short, blunt septal spines up to 1 mm long and 0·5 mm across at the base (Pl. 9, fig. 3). The coating has a general concentric disposition in the corallum but does not form obvious zones. Towards the axis the vesicles become less and less globose and the circular sections disappear. In the general region of the boundary between the zones of large and small vesicles the thickening abruptly increases. It may form a single broad somewhat ill defined concentric band extending well into the zone of larger vesicles and ringing a relatively narrow axial zone of lighter thickening about one-fifth the diameter across. In other sections this may grade into a series of relatively narrow concentric bands of thickening in the zone of larger vesicles. The thickening partly obscures the septal spines which are coarser here and are developed to within a short distance of the axis. Often isolated spots of sectioned septal spines occur in the immediately periaxial area. The larger vesicles average about 2 mm across periaxially and increase in size towards the axis.

In longitudinal section, the relative width of the zone of smaller dissepiments and the degree of eversion of its upper surface is seen to increase with increasing size. The vesicles gradually increase in size towards the axis and the septal spines are best developed just outside the zone of larger vesicles and heavy thickening. The spines may reach 1·7 mm in length. Their microstructure is not perfectly clear but they appear to consist of localized broad fans in the fibronormal material. At the inner edge of the zone of smaller vesicles the surface slope is about 50° to the horizontal. The larger vesicles are much thickened and may be completely obscured in a dense mass of sclerenchyme. Towards the edge of the zone the thickening can be seen as separate cones on the surface of the vesicles but the cones tend to merge in the axial area. The vesicles in the axial area do not exceed 3·5 mm across their bases, and are arranged with a shallow bowl-shaped surface across the axis.

Discussion. Birenheide (1964 : 23), in his comprehensive revision of the Devonian cystimorphs, made *Cystiphyllum americanum* a subspecies of the Middle Devonian species *Plasmophyllum secundum*. In particular he noted that larger examples of *P. secundum americanum* could scarcely be distinguished from the West European subspecies *P. secundum conistructum* Quenstedt. To judge from Birenheide's figures, however, and from a general comparison of American and German material, there would appear to be several points of difference. *Plasmophyllum secundum americanum* has much more regularly developed vesicles, both in size and shape, particularly in the peripheral areas of the corallum. Furthermore, the development of short blunt wedge-shaped septal spines, most conspicuous in the inner part of the zone of smaller vesicles, is a characteristic feature of *P. secundum americanum* but does not appear to be present in *P. secundum conistructum.* On the other hand, typical *P. secundum americanum*, for example R45098 figured here (Pl. 9, figs 1–4), compares remarkably well with Wedekind & Vollbrecht's (1931, pl. 17, figs 1–2) illustrations of *Paralytophyllum crassum* (Wedekind) from the Givetian of Germany. In particular, the development of septal spines and the size are more or less identical, as is the calice shape, although this appears to be more variable in *P. secundum americanum* as a whole. Birenheide (1964 : 28) listed *Paralytophyllum crassum* in his synonymy for *P. secundum pseudoseptatum* (Schulz). The fact remains that but for the geographical isolation, any sort of distinction between the American material and European *P. secundum* would be difficult to maintain. Birenheide's synonymy for *P. secundum americanum* is accepted uncritically.

Plasmophyllum sp.

(Pl. 9, figs 5–7)

1943 *Zonophyllum* sp. Wells: 98, pl. 10, figs 5, 6.

MATERIAL. R45095, R49259 (3154), PRI 24425 (PRI 24427 cut from same specimen). Caño Grande; Caño Grande Fm., early Middle Devonian (upper Onesquethaw).

DESCRIPTION. Small subcylindrical fragments 12–16 mm in diameter. The corallum may be strongly constricted at intervals as a result of rejuvenation.

In cross-section the vesicles appear rather flattened sub-semicircular and variable in size from about 0·5 mm to 5 mm across their bases. The epitheca and two or three concentric internal surfaces are heavily thickened with fibronormal sclerenchyme. The external wall thus varies between 0·6 and 1·5 mm in thickness. When it is thinner, short blunt septal spines can be distinguished extending inwards about 1 mm from the periphery and approximately 0·6 mm apart. Thickening of the wall tends to obscure these spines completely. Similar septal spines may or may not occur associated with inner zones of thickening. The vesicles show a general increase in size towards the axis but the gradation, although irregular, is more or less continuous and inner and outer size zones cannot be distinguished.

In longitudinal section, the vesicles slope axially and downwards at the periphery and flatten out across the axis giving a bowl-shaped calice. The upper surface of the vesicles is frequently thickened. At intervals up the length of the corallite the lumen is entirely filled by sclerenchyme, more heavily deposited at the periphery so that vesicular tissue is seen only infrequently to reach the epitheca unobscured.

Discussion. Wells (1943 : 98) originally described some of this material as *Zonophyllum* sp. Following Birenheide's (1964) revision of the cystimorphs, the Venezuelan material clearly belongs to the group of *Zonophyllum* he regards as congeneric with *Plasmophyllum*.

Wells (*op. cit.*) noted that the Venezuelan material was similar in structure to *Cystiphyllum conifollis* Hall (1876, pl. 30, figs 3–9) as redescribed by Fenton & Fenton (1938 : 232, fig. 20, pl. 23, figs 9, 10, pl. 24, figs 4–7). Unfortunately the Fentons did not section and figure Hall's type material, all of which looks from Hall's figures to be too highly cystose to be closely related to the Venezuelan species. On the other hand, one specimen figured by Fenton & Fenton (1938, pl. 24, figs 5–7) from the Hamilton Group (Moscow Fm.) of Leicester, N.Y. as *'Cystiphyllum' conifollis* looks extremely similar to the Venezuelan specimens and may indeed be conspecific with them. It seems best therefore neither to use the name *conifollis* nor to erect a new species until Hall's original material has been redescribed.

Order TABULATA Edwards & Haime 1850

Suborder FAVOSITINA Sokolov 1962

Family **FAVOSITIDAE** Dana 1846

Genus ***FAVOSITES*** Lamarck 1816

1816 *Favosites* Lamarck: 204.
1851 *Emmonsia* Edwards & Haime: 152, 245.
1939 *Favosites* Lecompte: 80, *cum syn.*
1953 *Favosites* Ross: 48, *cum syn.*
1960 *Favosites* Philip: 196.
1965 *Favosites* Stumm: 60.
1965 *Emmonsia* Stumm: 65.

Diagnosis. Massive, ramose, foliaceous or encrusting cerioid corals. Corallites generally contiguous, polygonal, of similar diameter throughout their length. Corallite walls unthickened internally, but may be variably dilated in a thin peripheral zone. Mural pores confined to corallite wall faces, usually one or two but may be three to a face, arranged in vertical series. Septa present in some species, may be variably developed usually as spines in vertical rows but also as septal striae. Squamulae also present in some species, with or without septal spines, and also may be variable in development. Tabulae usually complete and horizontal, frequently suspended in squamulate forms.

Type species (see Edwards & Haime 1850 : 60). *F. gothlandicus* Lamarck 1816 : 205 = *Specimen . . . corallinum Gothlandicum* Linnaeus 1745 : 39, fig. 27 and 1749 : 106, pl. 4, fig. 27.

Discussion. Considerable discussion of the genus *Favosites* has been published. It is sufficient here to state that the writer accepts Philip's (1960 : 190) opinion on the status of squamulae in *Favosites* and also considers that *Thamnopora* should be maintained as a distinct genus.

Favosites venezuelensis (Weisbord) 1926

(Pl. 10, figs 1, 2)

1926 *Pleurodictyum venezuelense* Weisbord: 6, pl. 1, figs 8, 9.
1943 *Thamnopora venezuelensis* (Weisbord) Wells: 99, pl. 10, fig. 10.

DIAGNOSIS. *Favosites*, apparently nodular in form, with monomorphic corallites, up to 2 mm diameter, having walls unthickened within the colony. Corallite walls heavily thickened in a subcalicular zone 5–7 mm deep so as to completely close the lumen in most cases. Squamulae present, particularly well developed in thickened zone. Mural pores uniserial, sporadically biserial, 0·3 mm diameter. Tabulae complete, horizontal, 7 in 5 mm.

HOLOTYPE. PRI 21597 (PRI 24428 same specimen). Loose block (?) in Caño del Norte; Caño Grande Fm., early Middle Devonian (upper Onesquethaw).

MATERIAL. R45079 (3121). Caño Grande; same horizon as holotype. R45101 (3182). Caño del Sur; same horizon as holotype.

DESCRIPTION. Nodular colonies; R45101 is partly crushed, 85 mm long and about 50 mm maximum diameter.

Internally, the corallites are polygonal in cross-section, 3 to 4 sided in immature stages and mainly 6 to 7 sided when mature. They range up to almost 2 mm diameter when measured between the axial plates of opposite walls but mature corallites average about 1·4 mm diameter. The corallite walls are thin with the axial plate about 0·01–0·02 mm thick coated on either side by fibronormal tissue 0·02 to 0·04 mm thick in mid-wall positions. The fibronormal tissue thickens slightly into the corners of the corallites which are slightly rounded. Mural pores appear sporadically in mid-wall or slightly offset positions. No definite indications of septal spines or squamulae are seen in cross-sections through the centre of the colony.

Tangential sections close to the colony surface show variable degrees of thickening of the corallite walls (Pl. 10, fig. 2). Thickening first builds up in the angles of the corallite walls so that the lumen becomes increasingly rounded. At the same level increasing signs of squamulae appear, of variable size with truncate or bluntly tapering ends. There are also very rare indications of what may be septal spines. Towards the colony surface, wall thickening may build up to almost or completely close the corallites. The mural pores however appear to be least affected by this excess thickening and even maintain close to their usual diameter when the corallites they connect are apparently closed. At the colony surface, the thickening rapidly diminishes leaving calices rounded and separated by walls about 0·3 mm thick at their midpoints.

In longitudinal section the tabulae are complete, flat or slightly arched or sagging, and fairly wide spaced 7 in 5 mm. They either cross from wall to wall or link facing squamulae. The squamulae are flat to very faintly trough-shaped plates directed horizontally in most cases. They are up to 0·8 mm long, 0·5 mm wide and become more strongly developed as wall thickening begins to build up where they average 0·6 mm apart vertically. Corallites are normal to the colony surface for about 10 mm or rather more of their length and the corallite walls start to thicken quite rapidly about 5–7 mm from the surface. Associated with the thickening, both squamulae and tabulae become more numerous, the former also becoming increasingly thickened. Mural pores are sectioned more frequently due to the thicker walls. They are large and circular about 0·3 mm diameter and usually 1 mm apart in single vertical rows. Most corallite walls show occasional doubling up of the pores with variable horizontal spacing. Many pores appear to be capped by squamulae but the relationship is apparently not invariable. In longitudinal section, the calices appear to be bowl or funnel shaped and 1 to 2 mm deep for the most part but there is considerable variability. Most but not all of them are floored by a zone where the infilling of the corallites is more or less complete.

Discussion. This description is based mainly on the new material collected by Bowen, particularly R45101, and considerably supplements the previous descriptions. In particular, the well developed squamulae in this species have not been recorded before.

The species should clearly be placed in *Favosites* as that genus is now understood. The character of the wall thickening in *F. venezuelensis* although apparently unique in its development is comparable with that seen in many other species of *Favosites* (for example see Ross 1953, pl. 21, fig. 6; Philip 1960, pl. 24, fig. 4), and is essentially a mature surface feature of the colony. In *Thamnopora* the corallites are more or less rounded throughout the colony.

F. venezuelensis shows some similarities with *Emmonsia radiciformis* (Stewart 1938 : 69, pl. 16, figs 8–10, *non* Rominger 1876 : 34, pl. 12) and to a lesser extent with *Emmonsia carmani* Stewart (1938 : 67, pl. 15, figs 1–3). Both these species from the Middle Devonian of Ohio, however, appear to be more intensely squamulate and lack the strong thickening of the distal corallite walls.

Favosites arbuscula Hall 1876

(Pl. 10, figs 3–6)

1876 *Favosites arbuscula* Hall, pl. 36, figs 1–9.
1953 *Favosites* (*Emmonsia*) *arbuscula* (Hall); Ross: 54, pl. 14, figs 2–9.
1965 *Emmonsia arbuscula* (Hall); Stumm: 65, pl. 64, fig. 13.

Diagnosis. Ramose *Favosites* with branches averaging 14 mm diameter. Corallites oblique or perpendicular to surface, 1·2 to 1·8 mm mean mature diameter. Walls 0·1 mm thick with little or no thickening at aperture. Mural pores 0·2 mm diameter, uniserial. Squamulae abundant, sometimes concentrated in distinct zones. Tabulae thin, often suspended from squamulae, 1–1·5 mm apart.

Material. R45102–3, R49264–5 (3182). Caño del Sur; Caño Grande Formation, early Middle Devonian (upper Onesquethaw).

Distribution. Middle Devonian (Hamilton Group and equivalent units) of eastern North America. Caño Grande Fm. (early Middle Devonian) of the Sierra de Perijá, Venezuela.

Description. Colonies ramose with branches averaging 14 mm diameter, close packed or diverging. Largest fragment 80 mm long branching twice in planes at right angles to each other.

In cross-section the corallites are three or four sided when immature, six or seven sided when mature. There is a tendency for mature and immature corallites to be arranged in a regular pattern. Mature corallite diameters reach 1·8 mm and average about 1·5 mm. Their walls are thin, the axial plate about 0·02 mm thick flanked on either side by fibronormal tissue 0·04 mm thick. There is only slight rounding of corallite angles internally. Mural pores are infrequently sectioned, always close to the mid-wall position and signs of septal spines or squamulae are extremely rare.

At the colony surface, corallite walls are slightly thickened up to about 0·25 mm from side to side and often irregularly scalloped or provided with very short stubby spines. The corallites are nearly all polygonal with rounded corners and are only rarely subcircular. Mural pores are sectioned more frequently and occasional signs of squamulae are seen.

In longitudinal section, the corallites diverge at a low angle to the axis of the branch and curve over to open at the surface somewhat obliquely. Internally corallite walls show slight irregular thickening and thinning with a more marked but only slightly thicker zone within 1 to 1·5 mm of the branch surface. Mural pores are infrequently sectioned up to 0·2 mm diameter and of indeterminate vertical spacing. Squamulae are present as generally unthickened plates of flat to shallow trough-shaped section, horizontally or slightly upwardly directed and about 0·5 mm long. They are concentrated about 0·25 mm vertically apart in distinct zones 1 to 2 mm deep and with a vertical frequency of 4 to 5 mm. The tabulae are complete, unthickened, flat to gently undulating and mostly wide spaced 1 to 1·5 mm but sometimes up to 4 mm apart. They are often suspended from the squamulae.

Discussion. The Venezuelan material appears to agree in most respects with *Favosites arbuscula* Hall as redescribed by Ross (1953 : 54). Whether or not *Favosites digitata* Rominger (1876 : 39, pl. 15) is conspecific with and therefore a senior synonym of *F. arbuscula* cannot be determined in the absence of a modern description and illustration of Rominger's species. For the present it seems preferable to accept the well described *F. arbuscula*.

The Venezuelan material possesses a combination of characters within the range of *F. arbuscula* but not matched exactly in any of Ross' (1953 : 55) subspecies. No new subspecies designation is felt to be justified, however, and the material is referred to *F. arbuscula sensu lato*.

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VII. APPENDIX—COMPOSITION AND LOCATION OF SAMPLES

The most accurate system for the location of samples available is by means of the Maracaibo Cathedral co-ordinates employed by Compañia Shell de Venezuela on their 1 : 10,000 topographic maps. The co-ordinates are in km. All the localities are in the northern part of the Sierra de Perijá, Zulia State, Venezuela and the locations of *in situ* samples are plotted in Text-figs 1 and 2.

Caño Los Guineos Formation

Caño Los Guineos section:

3849	*Heliophyllum halli*	S 11·32	W 97·58
	Heterophrentis (*H.*) *simplex*		
	Stereolasma sp.		
	Syringaxon sp.		

Caño Grande Formation

Caño Grande section:

3121	*Bowenelasma typa*	N 10·11	W 89·36
	Favosites venezuelensis		
	Heliophyllum halli		
3124	*Heliophyllum halli*	N 10·04	W 89·34
3126	*Heliophyllum wellsi*	N 10·02	W 89·32
3129	*Briantelasma oliveri*	N 9·99	W 89·28
3145	*Heliophyllum halli*	N 9·81	W 89·11
3149	*Bowenelasma typa*	N 9·70	W 89·10
	Heliophyllum halli		
3154	? *Bowenelasma breviseptata*	N 9·79	W 86·06
	Heliophyllum halli		
	Plasmophyllum sp.		
3157	*Bowenelasma typa*	N 9·81	W 89·04
	? *Briantelasma oliveri*		
	Heliophyllum halli		
	Plasmophyllum secundum americanum		

Caño del Sur section:

3182	*Favosites arbuscula*	N 9·56	W 88·78
	F. venezuelensis		
3199	*Bowenelasma breviseptata*	N 9·29	W 89·25
	Heliophyllum halli		
3221	*Briantelasma* sp.	N 9·05	W 89·79
	Heliophyllum halli		
	Plasmophyllum secundum americanum		

Caño del Oeste section (boulder):

3323	*Bowenelasma typa* *Briantelasma* sp. *Heliophyllum halli*	N 12·83	W 87·79

Caño Colorado section:

3618	*Bowenelasma typa* *Briantelasma oliveri* *Heliophyllum halli*	N 6·01	W 91·98
3619	*Bowenelasma breviseptata* *Heliophyllum halli*	N 6·01	W 91·98

Caño Grande Fm. or lower Caño de Oeste Fm.

Caño Pescado section (slipped block):

3539	*Cylindrophyllum elongatum*	N 6·32	W 89·83

Caño del Oeste Formation

Caño Grande section:

3243	*Hadrophyllum* sp. ? *Stewartophyllum* sp.	N 9·69	W 88·11

Río Palmar Formation

Caño del Norte section:

3495	? *Durhamina* sp.	N 16·97	W 85·97

Caño Colorado section:

3784	*Amplexizaphrentis sutherlandi*	N 3·11	W 90·47

? Río Palmar Formation

Caño Grande section (boulder):

3270	*Durhamina* sp. nov.	N 10·51	W 86·68

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PLATE 1

Syringaxon sp.

FIGS 1, 2. Cross-sections (slides). R45130b, a. ×6.
FIG. 3. Longitudinal section (slide). R45130k. ×6.
Caño Los Guineos; Caño Los Guineos Fm., early Middle Devonian.

?*Stewartophyllum* sp.

FIGS 4, 5. Cross-sections (slides). R45110b, a. ×2·5.
Caño Grande; Caño del Oeste Fm., early Middle Devonian.

Stereolasma sp.

FIG. 6. Cross-section (slide). R45129a. ×3.
FIG. 7. Longitudinal section in counter-cardinal plane; C on left (slide). R45129g. × 3.
Caño Los Guineos; Caño Los Guineos Fm., early Middle Devonian.

Hadrophyllum sp.

FIG. 8. Cross-section (polished surface). R49275. ×2·5.
Caño Grande; Caño del Oeste Fm., early Middle Devonian.

Amplexizaphrentis sutherlandi sp. nov.

FIG. 9. Cross-section (peel), early ephebic stage. R45127b (taken from holotype). ×3.

FIG. 10. Cross-section (slide), early neanic stage 16 mm below R45127b. R45127a (cut from holotype). ×3.

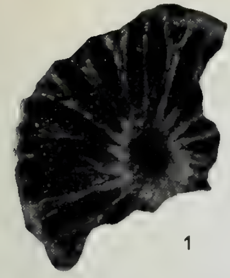
FIG. 11. Cross-section (peel), neanic stage 14 mm below R45127b. R45127d (taken from holotype). ×3.

FIG. 12. Longitudinal section in counter-cardinal plane; C on right (slide). R45127e (cut from holotype). ×3.

FIG. 13. Longitudinal section in counter-cardinal plane; C on left (slide). R49291b. ×2.
Both Caño Colorado; Río Palmar Fm., Lr. Pennslyvanian.

All cross-sections orientated with the cardinal septum at top centre.

PLATE 1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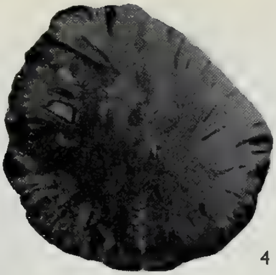
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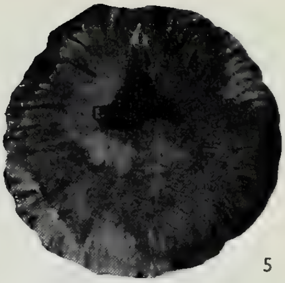
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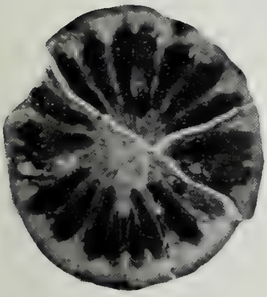
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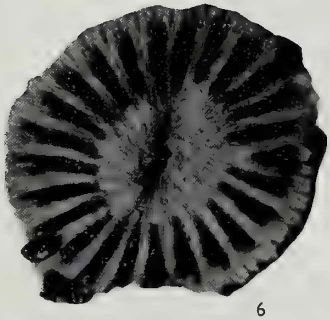
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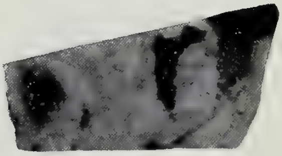
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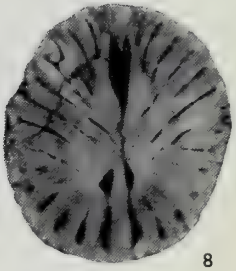
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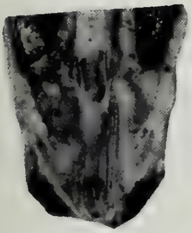
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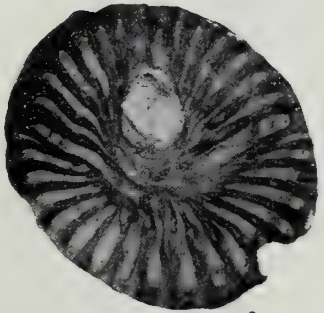
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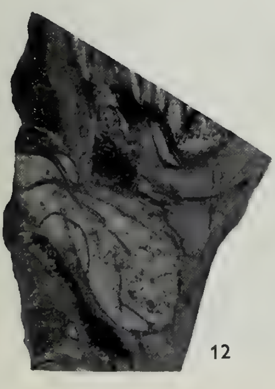
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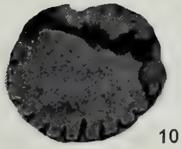
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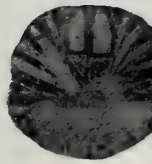
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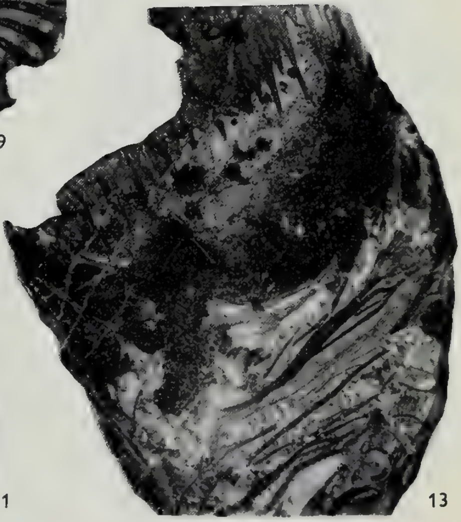
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PLATE 2

Bowenelasma typa gen. et sp. nov.

FIG. 1. Cross-section (slide), ephebic stage. R45094b (cut from holotype). ×2.

FIG. 2. Cross-section (peel), neanic stage. R45094d (taken from holotype). ×2.

FIG. 3. Longitudinal section in counter-cardinal plane; C on left (slide). R45094e (cut from holotype). ×2.

FIG. 4. Cross-section (slide), early neanic stage. R45100b. ×4.

FIG. 5. Cross-section (slide), ephebic stage. R45100a. ×2.

FIG. 6. Longitudinal section in counter-cardinal plane; C on left (slide). R45100c. ×2.

FIG. 7. Cross-section (slide), ephebic stage, to illustrate septal structure. R45094b (cut from holotype). ×6.

Both Caño Grande; Caño Grande Fm., early Middle Devonian.

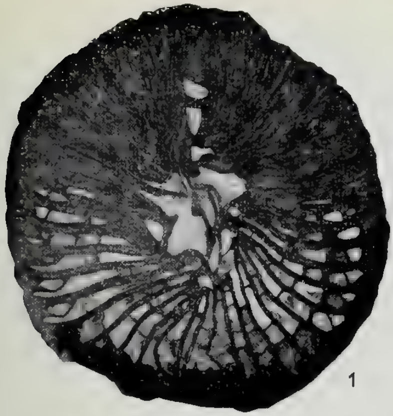
FIGS 8, 9. Cross-sections (peels), neanic stage. R45121f, e. ×2.

FIG. 10. Cross-section (slide), sub-calicular level. R45121a. ×2.

FIG. 11. Longitudinal section in counter-cardinal plane; C on left (slide). R45121h. ×2.

Caño Colorado; Caño Grande Fm., early Middle Devonian.

All cross-sections orientated with the cardinal septum at top centre.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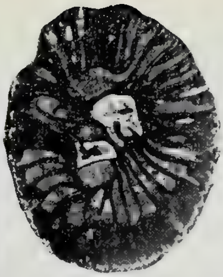
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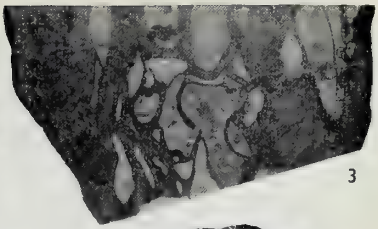
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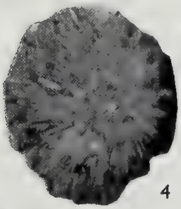
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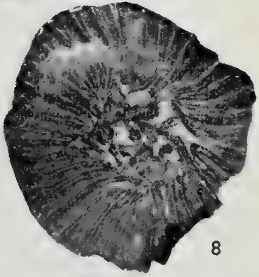
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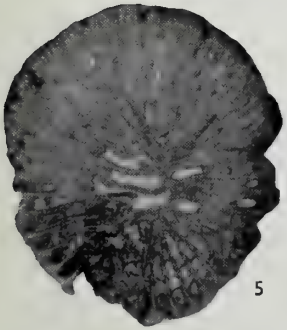
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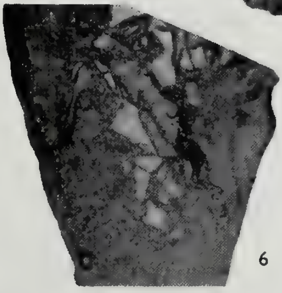
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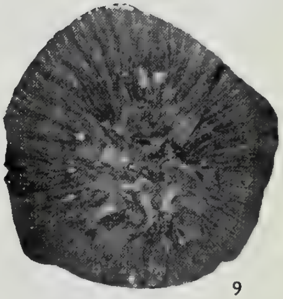
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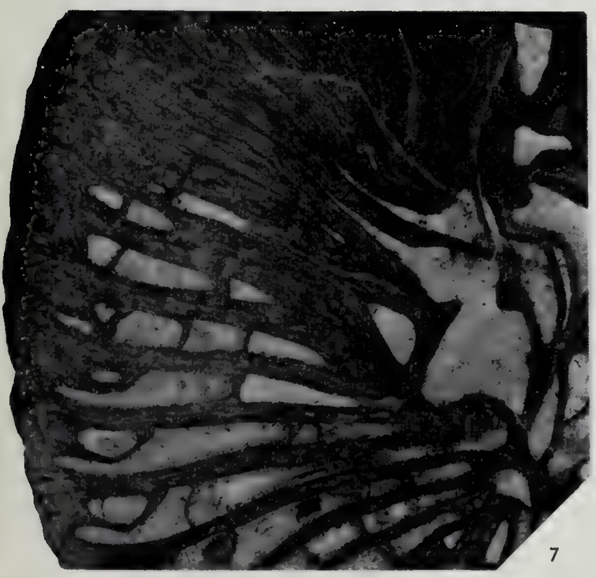
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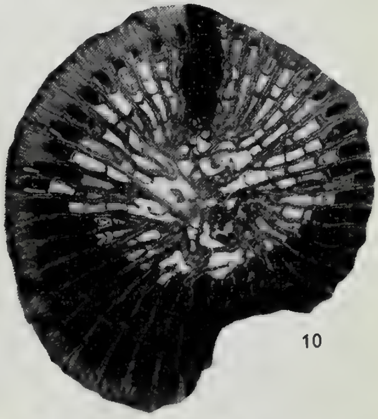
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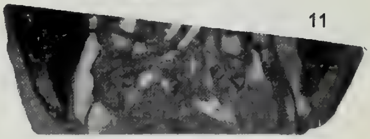
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PLATE 3

Bowenelasma breviseptata sp. nov.

FIGS 1, 2. Cross-section (slide), ephebic stage. R45123a (cut from holotype). Fig. 1 ×2; fig. 2, ×6.

FIG. 3. Cross-section (slide), neanic stage. R45123b (cut from holotype). ×2.

FIG. 4. Longitudinal section in counter-cardinal plane; C on left (slide). R45123d (cut from holotype). ×2.

Caño Colorado; Caño Grande Fm., early Middle Devonian.

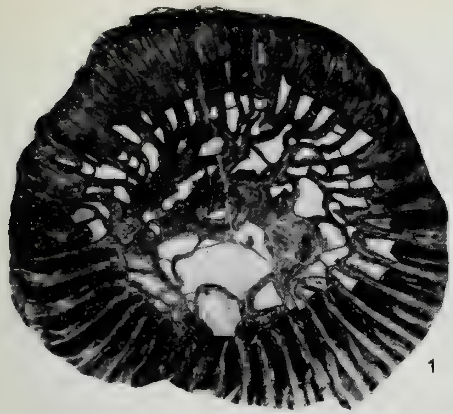
FIG. 5. Cross-section (peel), neanic stage. R45105c. ×2.

FIG. 6. Cross-section (slide), ephebic stage. R45105b. ×2.

FIG. 7. Longitudinal section (slide). R45105d. ×2.

Caño del Sur; Caño Grande Fm., early Middle Devonian.

All cross-sections orientated with the cardinal septum at top centre.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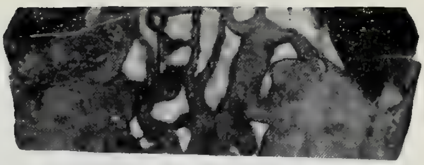
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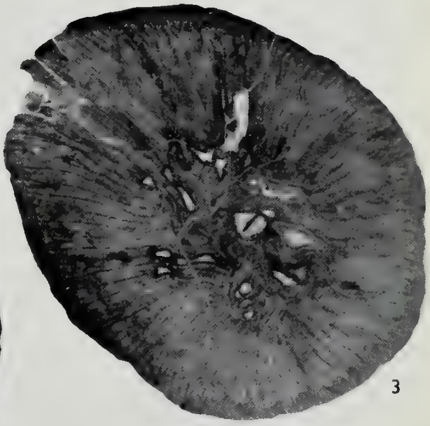
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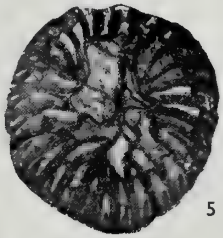
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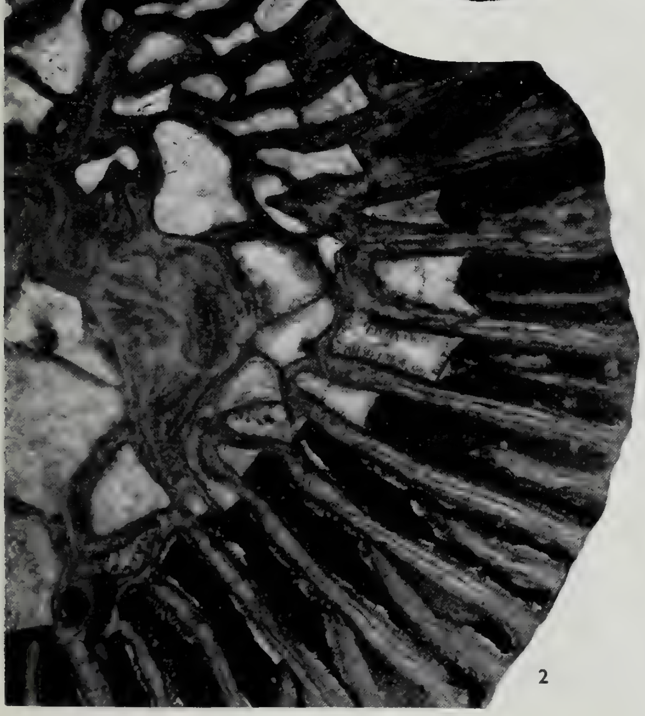
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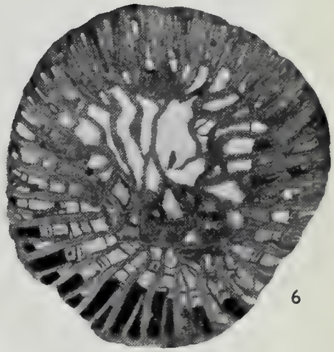
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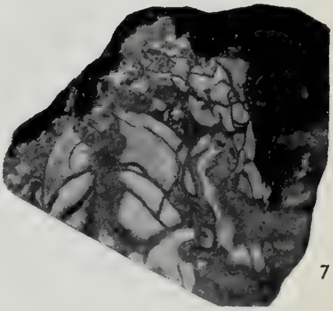
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PLATE 4

Briantelasma oliveri sp. nov.

FIGS 1, 2. Cross-section (slide), sub-calicular. R45090b (cut from holotype). Fig. 1, ×2; fig. 2, ×4.

FIG. 3. Cross-section (slide), ephebic stage. R45090a (cut from holotype). ×2.

FIG. 4. Longitudinal section (slide) in counter-cardinal plane; C on right. R45090e (cut from holotype). ×2.

FIG. 5. Cross-section (slide), neanic stage. R45091a. ×3.

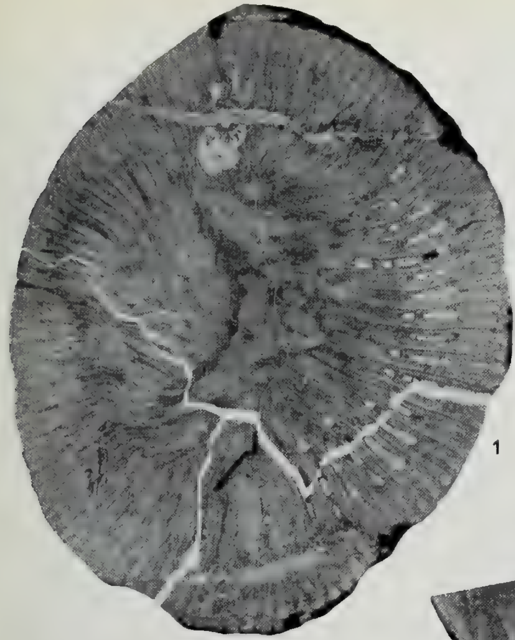
FIG. 6. Cross-section (slide), ephebic stage. R45091b. ×2.

Both Caño Grande; Caño Grande Fm., early Middle Devonian.

FIG. 7. Cross-section (slide), sub-calicular. R49290a. ×2.

Caño Colorado; Caño Grande Fm., early Middle Devonian.

All cross-sections orientated with the cardinal septum at top centre.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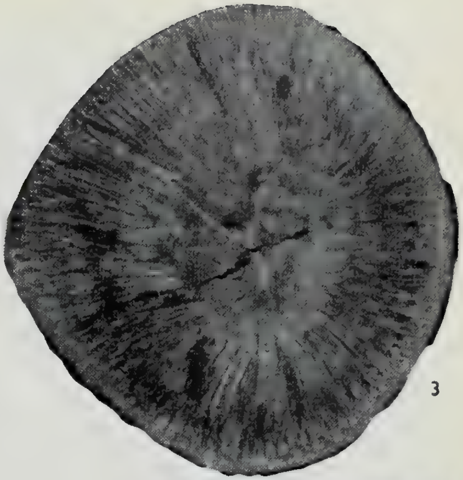
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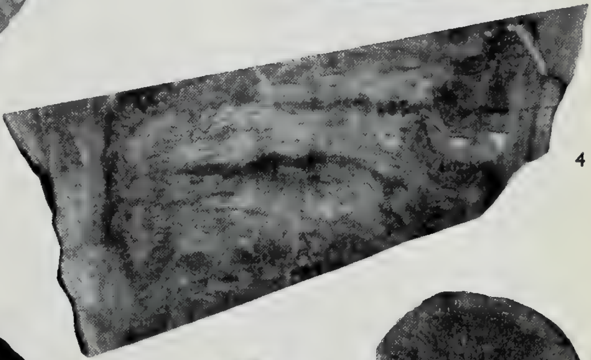
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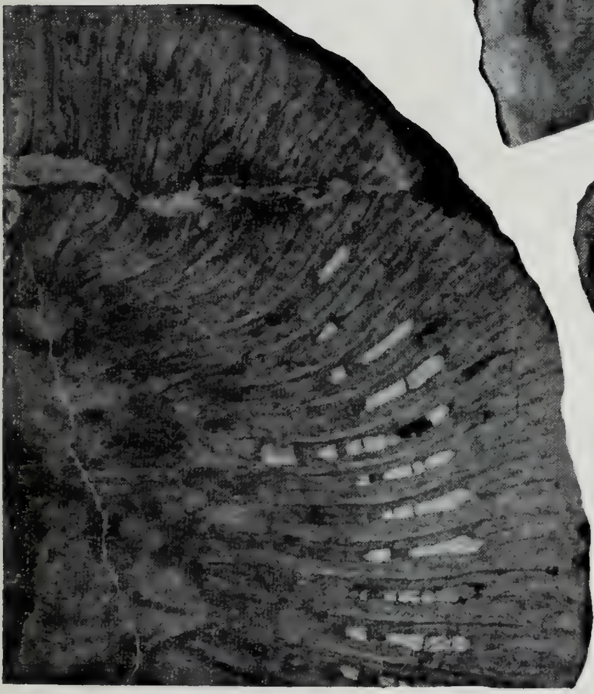
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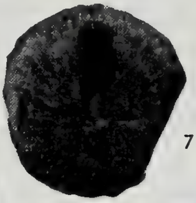
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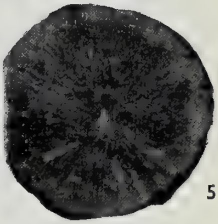
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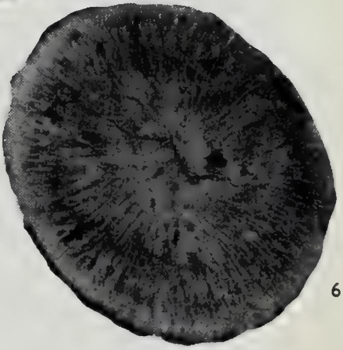
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PLATE 5

Heterophrentis (H.) venezuelensis (Weisbord)

FIG. 1. Cross-section (peel), ephebic stage. PRI 21594/PRI 24421 (taken from lectotype). ×2.
FIG. 2. Longitudinal section (peel). PRI 24421 (taken from lectotype). ×1·5.
?Loose boulder in Caño del Norte; Caño Grande Fm., early Middle Devonian.

Heterophrentis (H.) simplex (Hall)

FIG. 3. Cross-section (polished surface), ephebic stage. NYSM 360 (holotype). ×1·5.
Moscow, New York; Middle Devonian (Hamilton Group).

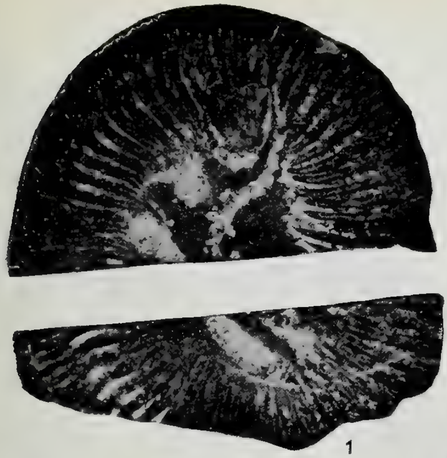
FIG. 4. Cross-section (polished surface), neanic stage. PRI 21593. ×1·5.
FIG. 5. Cross-section (polished surface), ephebic stage. PRI 21593. ×1·5.
?Loose boulder in Caño del Norte; Caño Grande Fm., early Middle Devonian.

Heliophyllum halli Edwards & Haime

FIG. 6. Cross-section (slide), ephebic stage. R45115a. ×2.
Loose boulder in Caño del Oeste; Caño Grande Fm., early Middle Devonian.

FIG. 7. Cross-section (slide), ephebic stage. R49289a. ×2.
FIG. 8. Longitudinal section in counter-cardinal plane; C on right (slide). R49289b. ×2.
Caño Colorado; Caño Grande Fm., early Middle Devonian.

All cross-sections orientated with the cardinal septum at top centre.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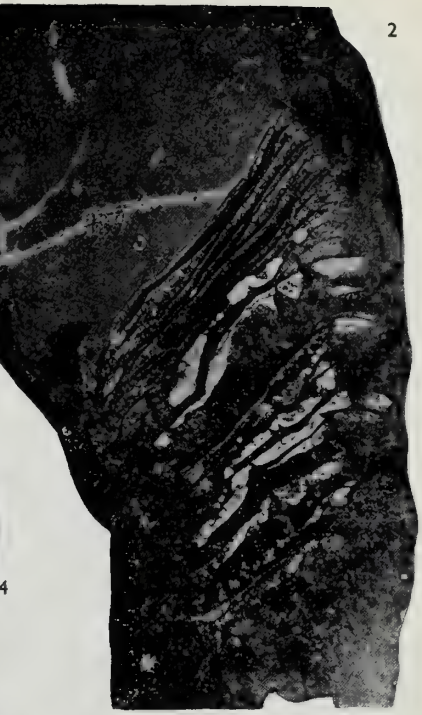
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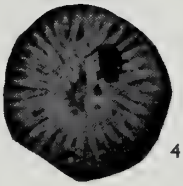
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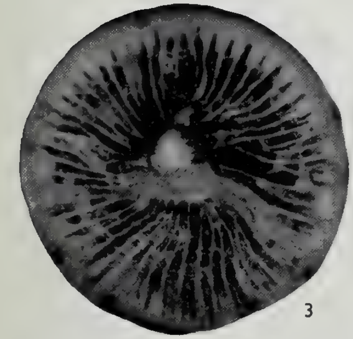
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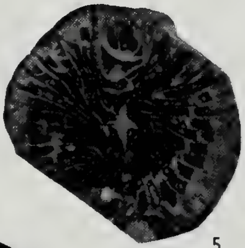
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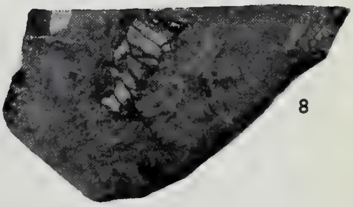
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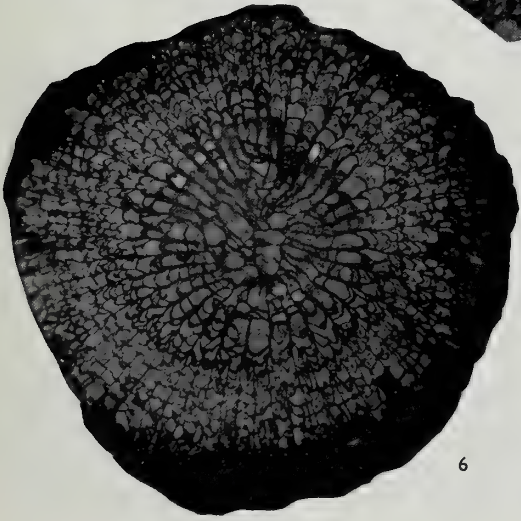
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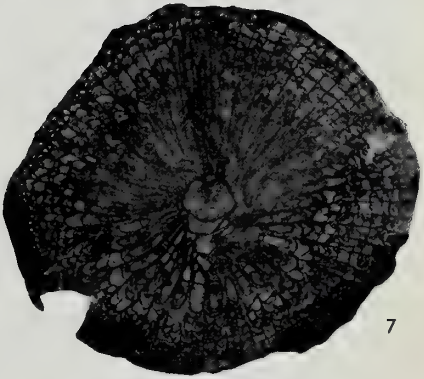
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PLATE 6

Heliophyllum halli Edwards & Haime

FIG. 1. Cross-section (slide), ephebic stage. R45104a. ×2.
FIG. 2. Cross-section (slide), neanic stage. R45104c. ×2.
Caño del Sur; Caño Grande Fm., early Middle Devonian.

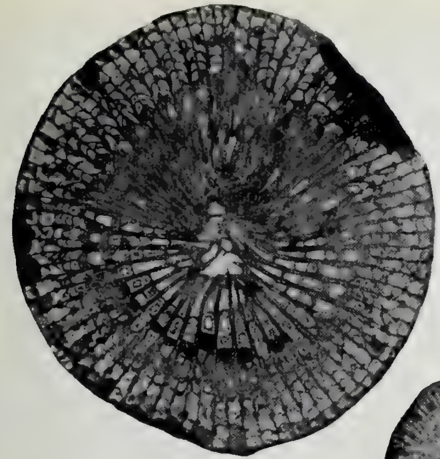
FIG. 3. Cross-section (slide), ephebic stage. R45092b. ×2.
FIG. 4. Longitudinal section in counter-cardinal plane; C on left (slide). R45092c. ×2
Caño Grande; Caño Grande Fm., early Middle Devonian.

FIG. 5. Cross-section (slide), ephebic stage. R49278a. ×2.
FIG. 6. Longitudinal section in counter-cardinal plane; C on left (slide). R49278d. ×2.
Loose boulder in Caño del Oeste; Caño Grande Fm., early Middle Devonian.

All sections orientated with the cardinal septum at top centre.

Heliophyllum wellsi sp. nov.

FIG. 7. Cross-section (slide), ephebic stage. R45088b (cut from holotype). ×1.
FIG. 8. Longitudinal section (slide). R45088e (cut from holotype). ×1·5.
Caño Grande; Caño Grande Fm., early Middle Devonian.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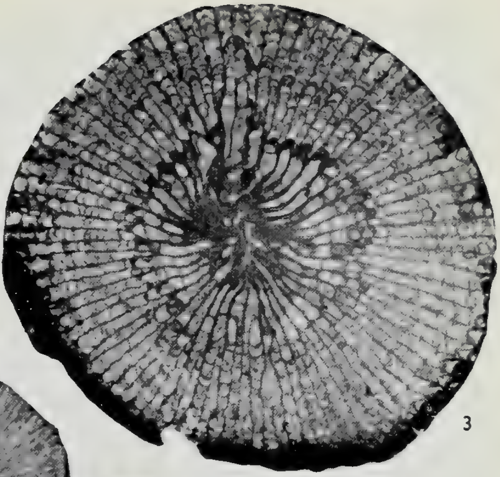
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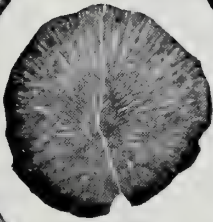
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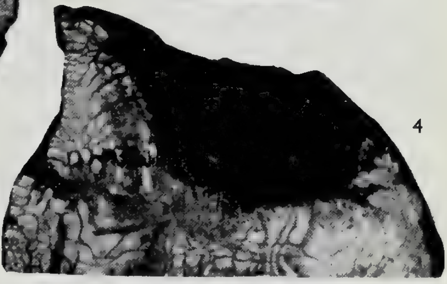
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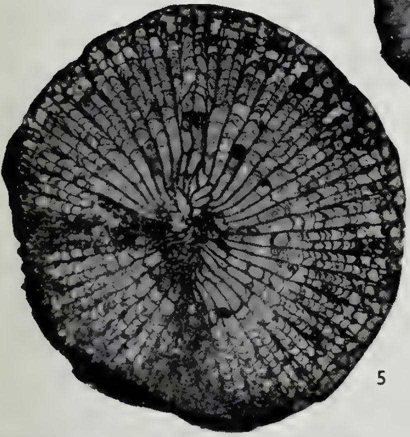
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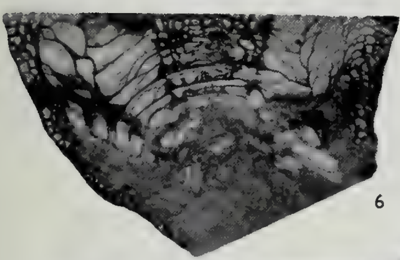
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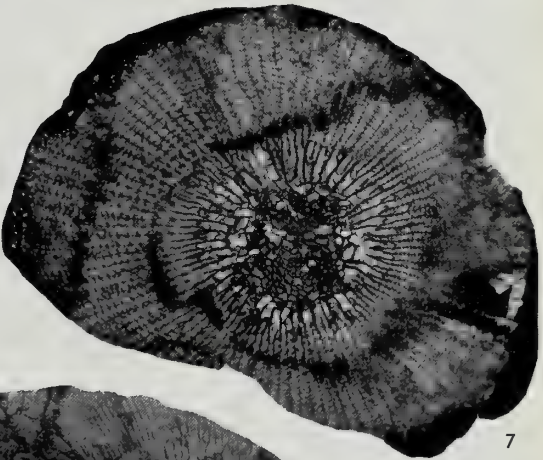
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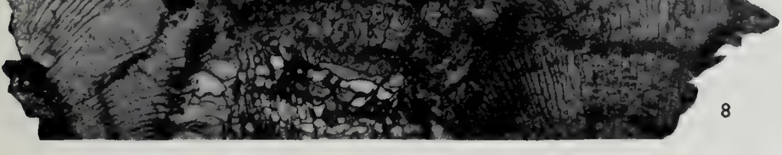
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PLATE 7

Heliophyllum wellsi sp. nov.

FIGS 1, 2. Cross-sections (slides), illustrating character of axial structure in ephebic stage. R45088a, b (both cut from holotype). ×2.

Caño Grande; Caño Grande Fm., early Middle Devonian.

Cylindrophyllum elongatum Simpson

FIG. 3. Cross-section (slide). R45116a. ×2·5.

FIGS 4–6. Longitudinal sections (slides). R45116h, j, g. ×2·5.

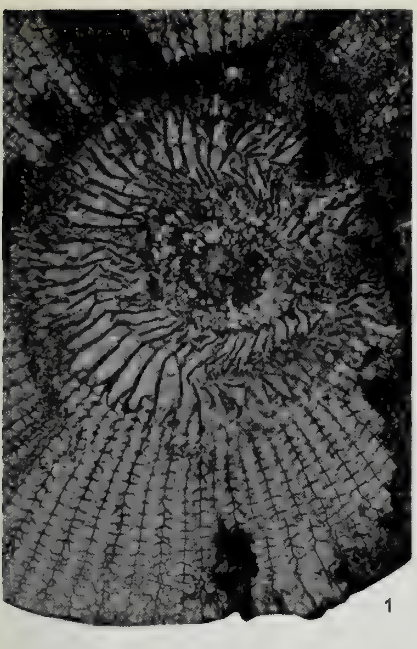
Loose block in Caño Pescado; either Caño Grande Fm. or low in Caño del Oeste Fm., early Middle Devonian.

?Durhamina sp.

FIG. 7. Cross-section (slide). R49285a. ×4.

FIG. 8. Longitudinal section (slide). R49285b. ×4.

Caño del Norte; Río Palmar Fm., Lr. Pennsylvanian.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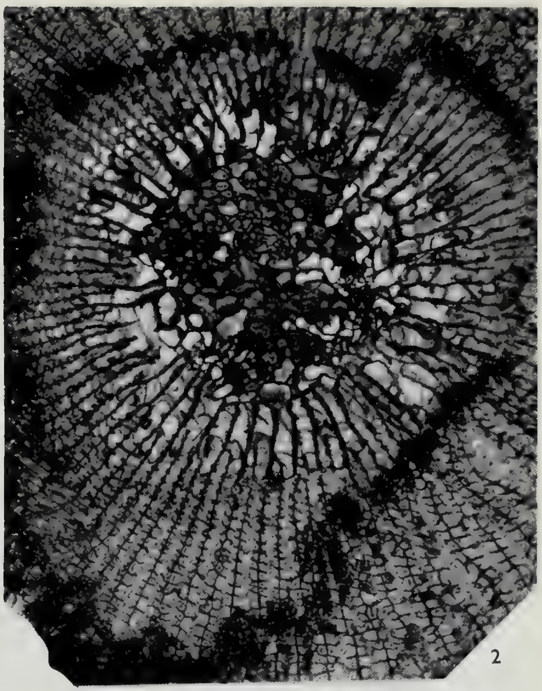
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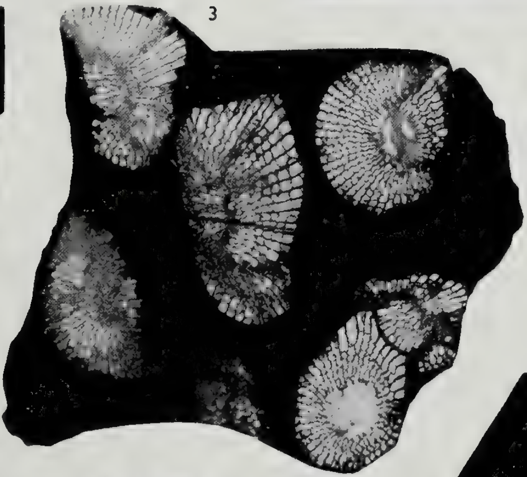
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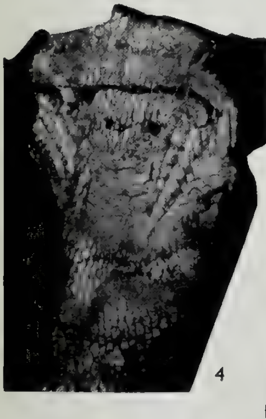
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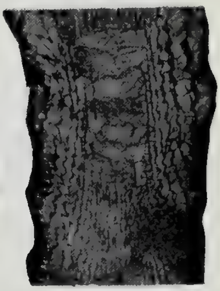
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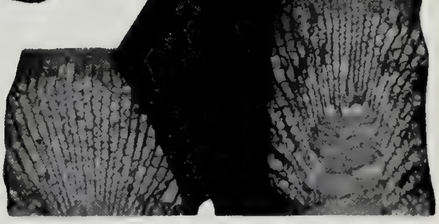
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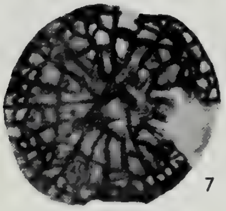
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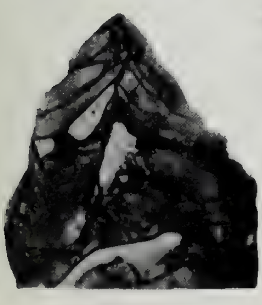
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PLATE 8

Durhamina sp. nov.

FIG. 1. Cross-section (slide) of corallite arrangement in colony. R49276b. ×1.

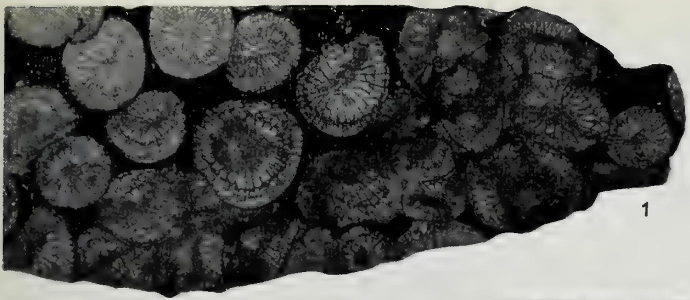
FIG. 2. Cross-section (slide) of corallite with third order septa. R49276b. ×6.

FIGS 3–4. Cross-sections (slides) showing variation in appearance of mature corallites. R49276c, a. ×2.

FIGS 5–7. Cross-sections (slide) of immature corallites. R49276a. ×4.

FIGS 8–10. Longitudinal sections (slides), fig. 8 showing increase. R49276h, i, j. ×2.

Loose block in Caño Grande; Carboniferous, (?Río Palmar Fm., Lr. Pennsylvanian).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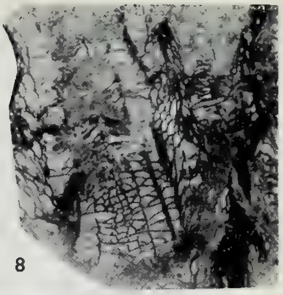
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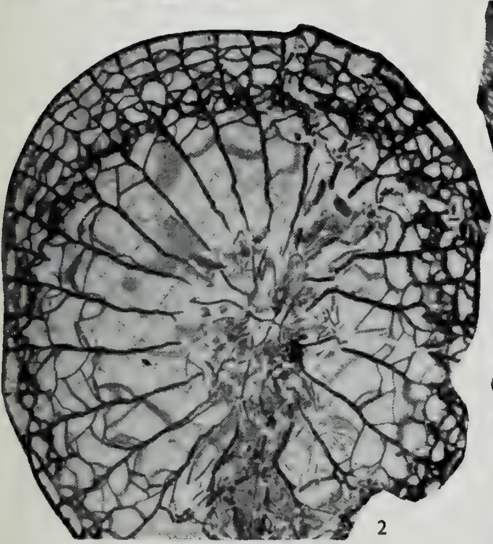
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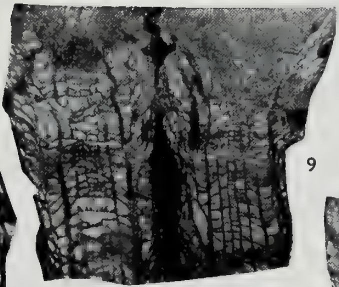
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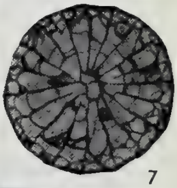
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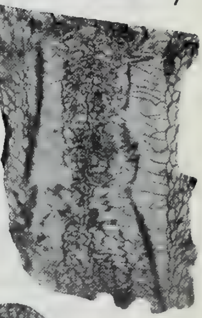
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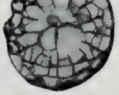
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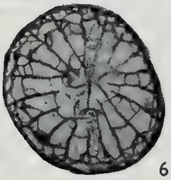
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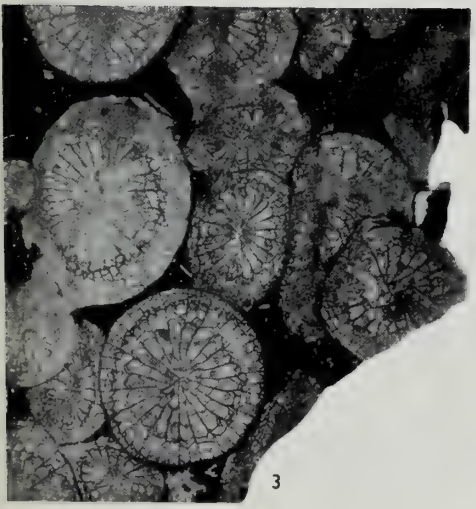
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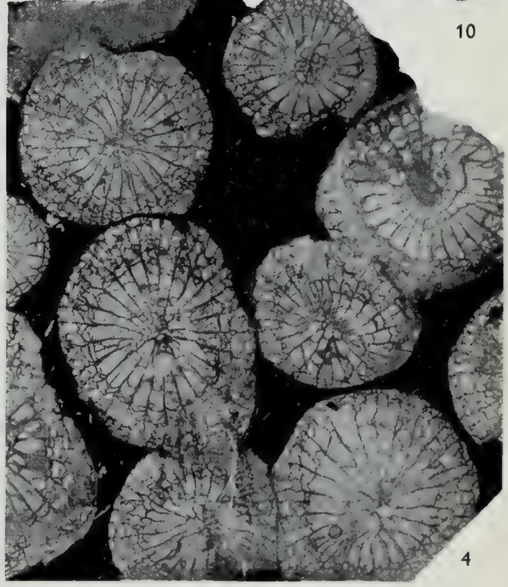

4

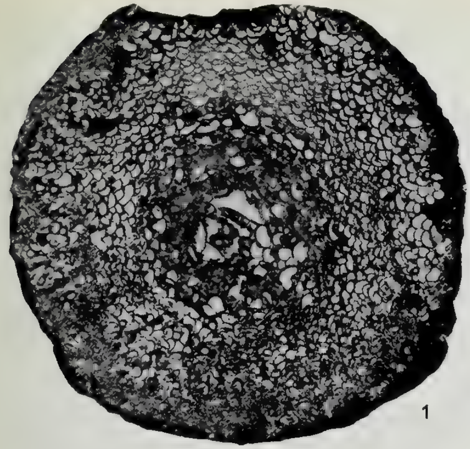
PLATE 9

Plasmophyllum secundum americanum (Edwards & Haime)

FIG. 1, 2. Cross-sections (slides). R45098b, c. ×1·5.
FIG. 3. Cross-section (slide) showing form and arrangement of septal spines. R45098b. ×6.
FIG. 4. Longitudinal section (slide). R45098d. ×1·5.
Caño Grande; Caño Grande Fm., early Middle Devonian.

Plasmophyllum sp.

FIGS 5–6. Cross-sections (slides). R45095a, b. ×3.
FIG. 7. Longitudinal section (slide). R45095c. ×3.
Caño Grande; Caño Grande Fm., early Middle Devonian.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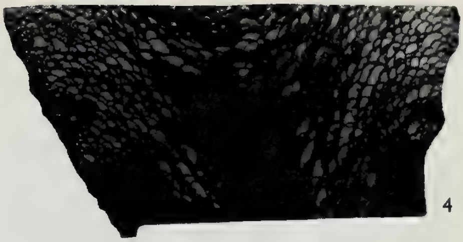
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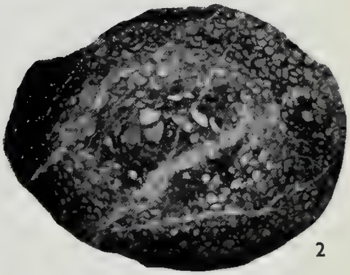
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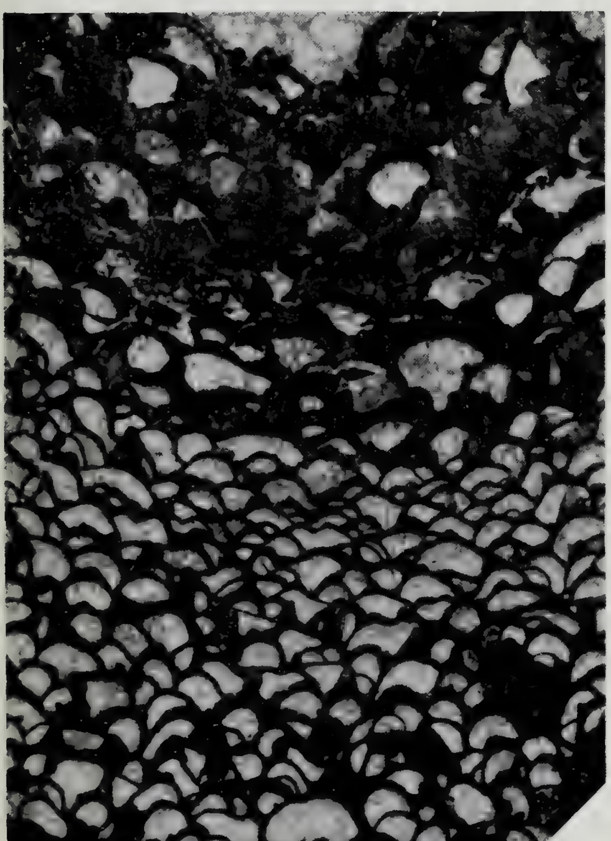
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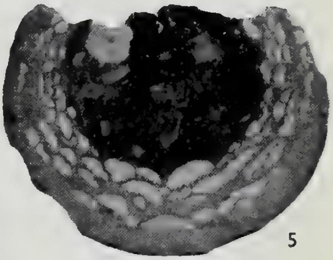
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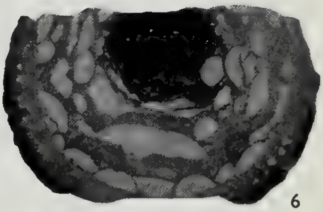
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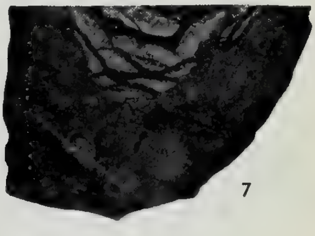
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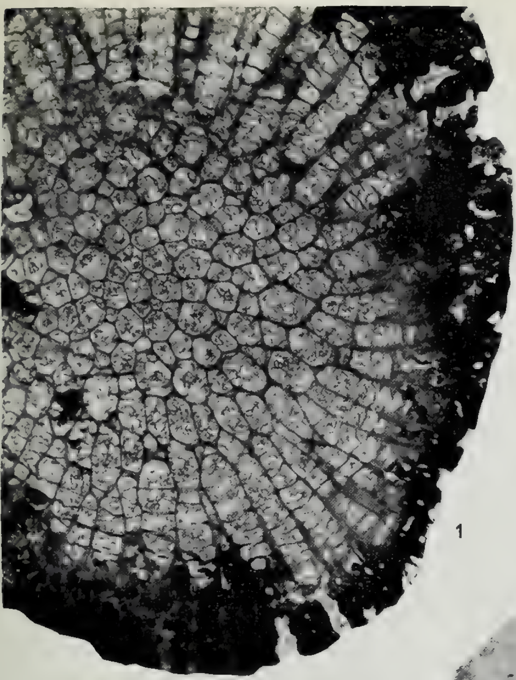
PLATE 10

Favosites venezuelensis (Weisbord)

FIG. 1. Cross and longitudinal sections (slide). R45101b. ×3.
FIG. 2. Tangential section (slide). R45101a. ×3.
Caño del Sur; Caño Grande Fm., early Middle Devonian.

Favosites arbuscula Hall

FIG. 3. Tangential section (slide). R45103a. ×3.
FIGS 4–5. Cross-sections (slides). R49264a, R45103b. ×3.
FIG. 6. Longitudinal section (slide). R49264b. ×3.
Caño del Sur; Caño Grande Fm., early Middle Devonian.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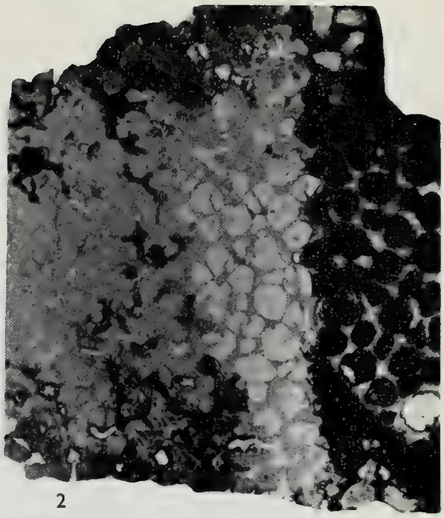
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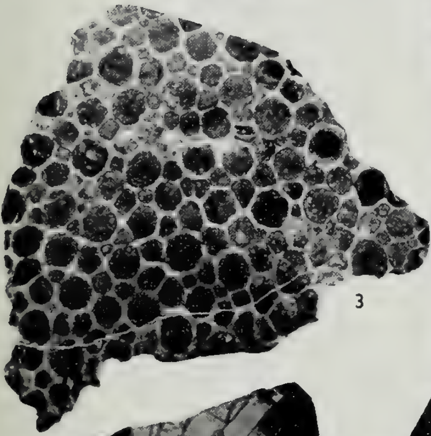
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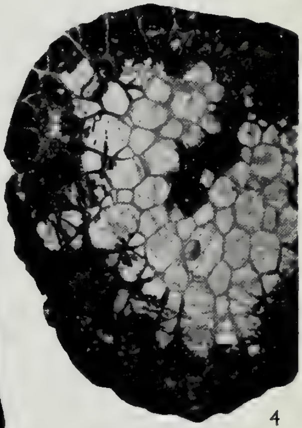
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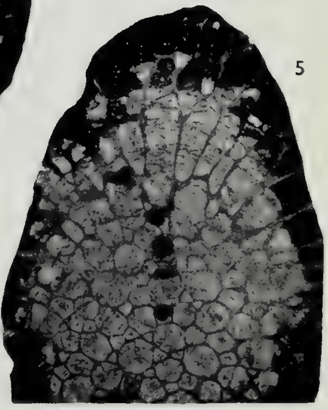
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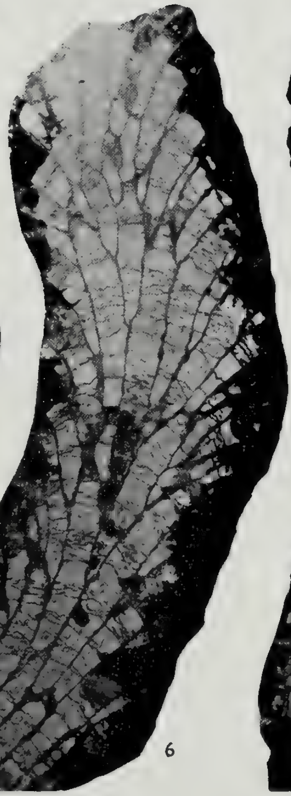
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PRODEINOTHERIUM FROM GEBEL ZELTEN, LIBYA

BRITISH MUSEUM
- 4 OCT 1973

J. M. HARRIS

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 23 No. 5
LONDON : 1973

PRODEINOTHERIUM FROM GEBEL ZELTEN, LIBYA

BRITISH MUSEUM
- 4 OCT 1973
NATURAL HISTORY

BY

JOHN MICHAEL HARRIS Xref
Centre for Prehistory and Palaeontology, Nairobi

Pp. 283–348; 5 *Plates*, 16 *Text-figures*

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THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 23 No. 5
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PRODEINOTHERIUM FROM GEBEL ZELTEN, LIBYA

By J. M. HARRIS

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SYNOPSIS

A large assemblage of vertebrate fossils has been collected from Miocene continental and near-shore marine lithosomes at the Gebel Zelten, Libya. Deinotheres were not prolific but are of interest in that they include the most complete skull yet discovered, plus the associated skull, mandible and partial skeleton of an immature individual. These are described and compared with other deinothere remains and with the postcranial skeleton of fossil and recent elephantoid proboscideans.

Features of the skull, skeleton and dentition indicate that the family Deinotheriidae possessed two genera and Ehik's taxon *Prodeinotherium* is resurrected for the earlier and more primitive genus to which the Gebel Zelten specimens belong. The facial region of the Libyan *Prodeinotherium* skull has a downcurved rostrum that is modified to bear a proboscis. The occipital region, basicranium and anterior cervical vertebrae are adapted to impart a powerful downward thrust to the tusks. The cheek teeth are separated into an anterior crushing battery and a posterior shearing battery.

The postcranial skeleton of *Prodeinotherium* and *Deinotherium* exhibit graviportal adaptations for support of the body weight. The atlas and axis vertebrae of deinotheres are distinctive and other differences in the postcranial skeleton from that of elephantoids may be detected. The scapula and foot bones of *Prodeinotherium* may be readily recognized but the long bones resemble those of *Elephas*. More advanced characters shown by *Deinotherium* include reduction of the scapular spine, shortening of the femur, elongation of the manus and pes, and reduction of the first digit thus leading to functional tetradactyly. These may all be interpreted as cursorial adaptations.

I. ABBREVIATIONS AND ACKNOWLEDGEMENTS

Individual specimens from Gebel Zelten are referred to by their University of Bristol accession numbers, e.g. 6404 : 44, 6418 : 20 (M.26665). Specimens of *Deinotherium giganteum* from Höwenegg, Germany, and currently at the Johannes Wurtemberg Universitaat, Mainz, had not been given permanent accession numbers at the time of writing and are referred to in tables of measurements as 'Höwenegg'. Recent specimens of *Loxodonta africana* used for comparison in the section on the axial skeleton include OM 2209 from the National Museum of Kenya and 1961.8.9.82 from the British Museum (Natural History). Comparison between the appendicular skeleton of *Prodeinotherium* and *Elephas maximus* was based on the skeleton of an Indian elephant in the University of Bristol Department of Geology (catalogue number U.B.20189). Deinothere material with KNM catalogue numbers is from the Centre for Prehistory and Palaeontology, Nairobi. The catalogue numbers of mammalian specimens from the British Museum (Natural History) are prefaced by B.M.(N.H.)M. or (in tables of measurements) M. In the tables, measurements are given in cms. unless otherwise stated; * = approximate measurement, + = incomplete specimen.

This paper formed part of a Ph.D. thesis from the University of Bristol that was supervised by Dr R. J. G. Savage for whose help and encouragement I am very grateful. The work was financed by a grant from N.E.R.C. I am grateful also to Mrs D. M. Leakey who read and criticised the manuscript.

Prodeinotherium skull M.26665 was prepared by Mr A. Rixon in the Department of Palaeontology, British Museum (Natural History). Deinothere material from the 1964 and 1966 University of Bristol expeditions was prepared by Mr. M. White of the Department of Geology, University of Bristol. The photographs were prepared by Mr R. Godwin and line drawings of the postcranial material by Mrs M. Clapp.

Field work in Libya was made possible by generous co-operation from Esso Standard Libya and Oasis Oil Company of Libya Inc.

I am indebted to the staff of the various institutions that have permitted me to examine material in their collections, and especially the late Professor C. Arambourg (Institut de Paleontologie, Paris), Professor H. Tobein (Johannes Wurtemberg Universitaat, Mainz), Professor R. Dehm (Institut für Paläontologie, Munich), Dr E. Aguirre (Museo de Sciencias Naturales, Madrid), Dr L. S. B. Leakey (Centre for Prehistory and Palaeontology, Nairobi), and Dr A. Sutcliffe (Department of Palaeontology, British Museum (Natural History)).

II. INTRODUCTION

THE Gebel Zelten is an elongate mesa lying approximately 200 kms inland from the Gulf of Sirte and is bounded by the co-ordinates 19½°–20½°E and 28–29°N. The gebel extends for some 140 kms in a northwest-southwest direction. It attains a height of some 40–60 metres at its western extremity but gradually decreases in elevation towards the east until it merges with the Calenscio Serir. At the eastern extremity of the gebel the northern and southern scarps are separated by a distance of some 50 kms. The scarps converge towards the west and near the centre of the gebel they are only 8 kms apart. West of this point the southern scarp diverges sharply from the northern before merging at the extreme western extremity (see text-fig. 1). The Gebel Zelten is deeply dissected by wadis that often reach 3 kms in length. Most of the vertebrate sites are located in branches of the wadi systems.

The rocks exposed at the Gebel Zelten are of Miocene age and were attributed by Selley (1966) to the Marada Formation. The rocks represent the mixed fluvio-marine facies of the southern part of the Sirte Basin. The succession at Gebel Zelten is predominantly of sandstone, sandy shales and shales, the units dipping northward at an angle of about six seconds (Doust, 1968). According to Doust, the base of the section at the northern scarp consists of intertidal and fluviatile sands and shales that pass upward into bioturbated calcarenites and calcsilicates representing intertidal and subtidal facies. The top of the succession comprises calcareous crossbedded sandstones from an estuarine channel facies. On the southern scarp a mixed intertidal and fluviatile facies passes upwards into intertidal sediments that are ultimately overlain by the estuarine channel facies. Detailed discussions of the geology are given in Selley (1966, 1967, 1968), Doust (1968), and Magnier (1962, 1968).

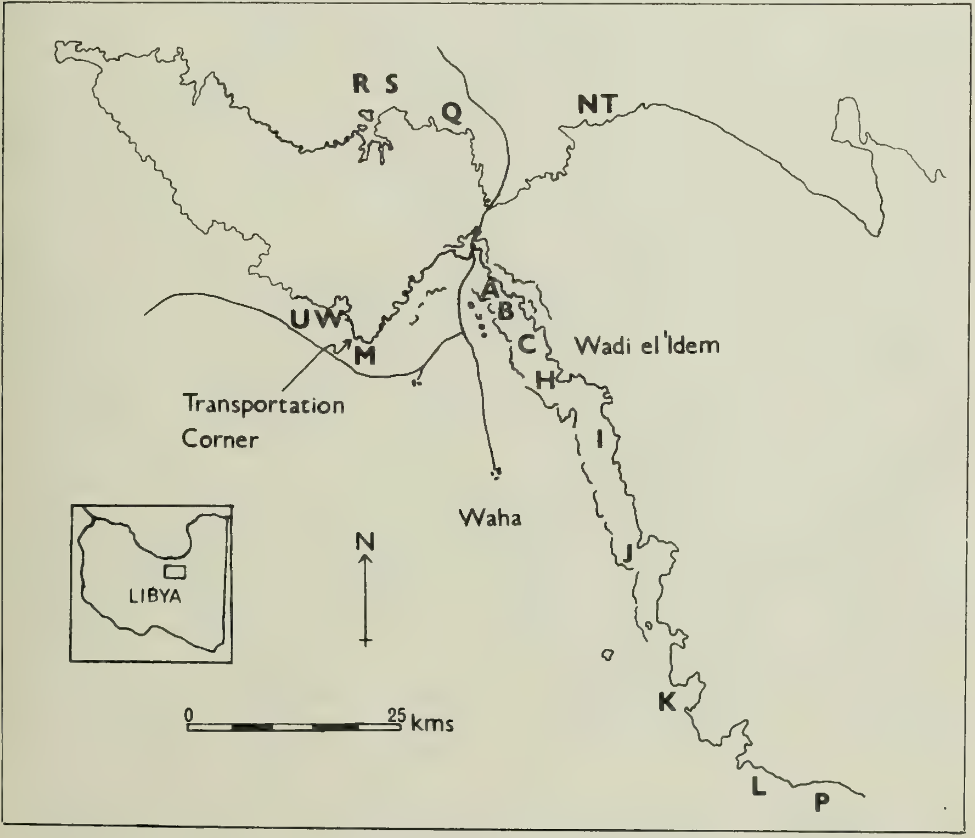


FIG. 1. Vertebrate localities of the Gebel Zelten.
Sites D, E, F and G are located between sites C and H.

The vertebrate fauna of the Gebel Zelten was discovered in 1958 by personnel of the Compagnie des Petroles Total (Libye) during a regional reconnaissance of Libya (Magnier, 1962). In December 1960 an expedition from the Museum National d'Histoire Naturelle, Paris, visited Gebel Zelten to exploit the vertebrate remains (Arambourg & Magnier, 1961). Only an area 20 km long at the centre of the northern scarp of the Gebel was prospected in detail but vertebrate specimens were collected from all exposures examined. The material retrieved is currently housed in the Institut de Paléontologie, Paris. A faunal list was given by Arambourg and Magnier (1961), and later revised by Arambourg (1963b). Of the elements listed only *Bunolistriodon massai* has been described in detail (Arambourg, 1963a) but preliminary descriptions of *Afrocyon burolleti, Prolibytherium magnieri, Mastodon pygmaeus* and an aeopyornithid tibia have been published (Arambourg 1961a, 1961b).

From 1964, expeditions from the University of Bristol under the leadership of Dr R. J. G. Savage have systematically collected vertebrate material from Gebel Zelten. Exploitation of the southern scarp was undertaken in 1964 and of the northern scarp in 1966. The 1967 and 1968 expeditions expanded and consolidated the results of earlier investigations. In all, well over a thousand specimens, representing several tons of unprepared material, have been collected by University of Bristol parties. This is in addition to the material collected by the 1960 French expedition and to the specimens donated by oil company personnel to the British Museum (Natural History) and American Museum of Natural History. A list of the faunal elements collected was given in Savage and White (1965) and revised in Savage (1967) and Selley (1968).

Most of the vertebrate fossils have been collected from channels and flood plains of the fluviatile facies, though remains are not infrequent in the tidal flat facies. At the time of writing 24 sites had been discovered and these were assigned letter prefixes in alphabetical order of discovery (see fig. 1). Permanent site numbers and other pertinent data are now on file in the Department of Geology, University of Bristol. All the Gebel Zelten sites occur near the base of the exposed section and range in areal extent from one to ten acres. A table showing the distribution of the Gebel Zelten mammal fauna by sites was given by Savage (in Selley, 1968).

Desio (1935) referred the rocks on the south side of the Gebel Zelten to the Aquitanian stage and those on the north scarp to the Burdigalian. The vertebrate fauna was allocated a Burdigalian age by Arambourg (1963b) although it is not clear whether this age was based on the mammalian elements or on the marine invertebrates. Savage and White (1965) confirmed a Burdigalian age for the mammals, and Savage (in Selley, 1968) later refined the age of the fauna to early Burdigalian or even late Aquitanian. Definite conclusions on the age of the Gebel Zelten assemblage must necessarily be delayed until all the mammalian groups represented have been thoroughly investigated. To date only the carnivores (Savage, 1973) and giraffoids (Hamilton, 1973) have been completed.

The Gebel Zelten deinothere skulls are not only the earliest skulls, though not the earliest deinothere specimens (which are from East Africa), but are also unusually complete. The best preserved specimen (6418 : 20) was collected in 1966 and was deposited in the British Museum (Natural History). The accession number of the specimen is M.26665. All the permanent teeth are erupted and show wear but the zygomatic, squamosal, auditory and pterygoid regions are poorly preserved.

A virtually complete skull of an immature individual was collected by the writer from Site D in 1967. This specimen (6404 : 44) was completely buried and was only discovered during the excavation of deinothere limb material, for which purpose site D had been revisited. The skull was lying on its side (the only deinothere skull from Gebel Zelten that was not lying upside down) and had been slightly deformed by compaction after burial. The bone was in an extremely fragile state and the right zygomatic arch disintegrated during excavation. The occipital region fragmented and became partially deformed during transportation to Bristol. Permanent P^3–M^1 are fully erupted but only M^1 shows wear. M^2 is only partly erupted. The squamosal, auditory and orbital regions are better preserved than in M.26665. Several of the facial sutures are still unfused. The mandible (6404 : 45) and much of the skeleton belonging to this individual (M.26667a–l) were excavated from the adjacent part of site D.

An incomplete deinothere skull (6404 : 14) and much of a mandible (6404 : 13) were collected in 1964 from within a few yards of skull 6404 : 44. Unfortunately skull 6404 : 14 was broken in transit from the Gebel Zelten and only the premaxilla, jugal and dentition are now in a reasonable state of repair. The teeth of the 1964 specimens are in different stages of eruption and wear and are not thought to belong to one individual.

The 1968 Bristol expedition to Gebel Zelten and Dor el Talha discovered an incomplete and partly crushed skull at Gebel Zelten site L. Pieces of this skull were collected but all except a fragment of the inferior half of the occiput are still in Libya. The ventral edges of the lateral wings of the squamosal are better preserved on this specimen than on M.26665. Two other partly eroded skulls were discovered at site R by the 1966 expedition. These were allocated field numbers (6418 : 4, 6418 : 19) but have yet to be collected.

In addition to the deinothere postcranial material from site D, a cuneiform and isolated vertebrae have been collected from other Gebel Zelten sites. Gebel Zelten deinothere material is appreciably smaller than, and differs morphologically from, equivalent specimens of *Mastodon angustidens* from Gebel Zelten. In the ensuing descriptions, comparisons with recent elephant remains are based on vertebrae of *Loxodonta africana* from the British Museum (Natural History), the manus and pes of *L. africana* from the Osteology Department of the Centre for Prehistory and Palaeontology, Nairobi, and fore and hind limb material of *Elephas maximus* in the University of Bristol collections. Comparative deinothere material includes the partial skeleton of '*Deinotherium bavaricum*' in the Naturhistorisches Museum of Vienna, the partial skeleton of *D. giganteum* from Valladolid in the Museo de Sciencias Naturales of Madrid, and carpals and tarsals of *D. giganteum* from Höwenegg in the University of Mainz collections.

Conclusions on deinothere taxonomy, morphology and functional anatomy were made after viewing specimens in the following institutions: British Museum (Natural History), London; Centre for Prehistory and Palaeontology, Nairobi; Department of Geology Museum, University of Bologna; Museo de Sciencias Naturales, Madrid; Institut de Paleontologie, Paris; Naturhistorisches Museum, Vienna; Institut für Paläontologie und Historisches Geologie, Munich; Hessisches Landesmuseum, Darmstadt; Naturhistorisches Museum, Mainz; Institut für Paläontologie, Johannes Wurtemberg Universitat, Mainz; Naturhistorisches Museum, Wiesbaden. Extensive use has been made also of data given by Bergounioux & Crouzel (1962a, 1962b), Dehm (1963), de Pauw (1908), Graf (1957), McInnes (1942), Pacheco (1930), Palmer (1924), Sahni & Tripathi (1957), Stefanescu (1897, 1907), and Tobein (1962).

The results of these investigations suggest that some revision of deinothere systematics is necessary. Diagnoses are given at the beginning of the section on systematic description because the Gebel Zelten deinotheres do not appear to belong to the type genus.

TABLE I

Deinothere specimens from Gebel Zelten

Field number	Accession number	Description
6401 : 1		Left M^3
6401 : 4		Right maxilla with P^3–M^3
6404 : 13		Mandible with tusks and cheek teeth
6404 : 14		Skull fragments with dentition
6404 : 30	M.26667a	Distal end of fibula
6404 : 31	M.26667b	Right ulna
6404 : 32	M.26667c	Proximal end of right humerus
6404 : 33	M.26667d	Right femur
6404 : 34	M.26667e	Left ulna
6404 : 36	M.26667f	Right scapula
6404 : 37	M.26667g	Left innominate
6404 : 38	M.26667h	Left rib head
6404 : 39	M.26667i	Right neuropophysis of 3rd cervical vertebra
6404 : 41	M.26667j	Proximal and distal end of left radius
6404 : 44		Immature skull
6404 : 45		Fragmented immature mandible
6404 : 46	M.26667k	Distal end of right humerus
6404 : 47	M.26667l	Distal end of left humerus
6405 : 98		Left cuneiform
6409 : 41		M^2 fragment
6410 : 2		Deciduous P_4
6412 : 10		Tuskless mandible with worn cheek teeth
6412 : 39		Left M_2
6412 : 40		Left M_1
6412 : 54		Left P^4
6413 : 18		Left M^3
6416 : 120		Tusk tip
6416 : 130		Tusk
6418 : 20		Adult skull
6418 : 22		Mandible with tusks and cheek teeth
6419 : 15		Atlas vertebra
6419 : 16		Tusk alveoli
6419 : 17		Enamel fragment
6421 : 2		Left M^2
6421 : 15		Molar fragment
6423 : 13		Enamel fragment
6423 : 45		Enamel fragment
6423 : 56		Enamel fragment
**6424 : 79		Axis vertebra

** = Site unknown

III. SYSTEMATIC DESCRIPTIONS

Order PROBOSCIDEA Illiger, 1811

Suborder DEINOTHERIOIDEA, Osborn, 1921

Family ***DEINOTHERIIDAE*** Bonaparte, 1845

DIAGNOSIS. Large herbivorous graviportal mammals. Dental formula $\frac{0.0.3.}{1.0.3.}$ for the deciduous teeth and $\frac{0.0.2.3.}{1.0.2.3.}$ for the permanent dentition; DP$^2_2$ and P$^3_3$ with well developed external crest; DP$^4_4$ and M$^1_1$ trilophodont; the remainder of the cheek teeth are bilophodont. Horizontal tooth replacement not developed so that all permanent teeth may be erupted at the same time (cf. elephantoids). Mandibular symphysis and lower tusks curved downwards so that the tusk tips are vertically or nearly vertically aligned. Skull low with deep rostral trough, retracted external nares, low orbit, inclined occiput, high occipital condyles, elongate paroccipital processes, and diplöe.

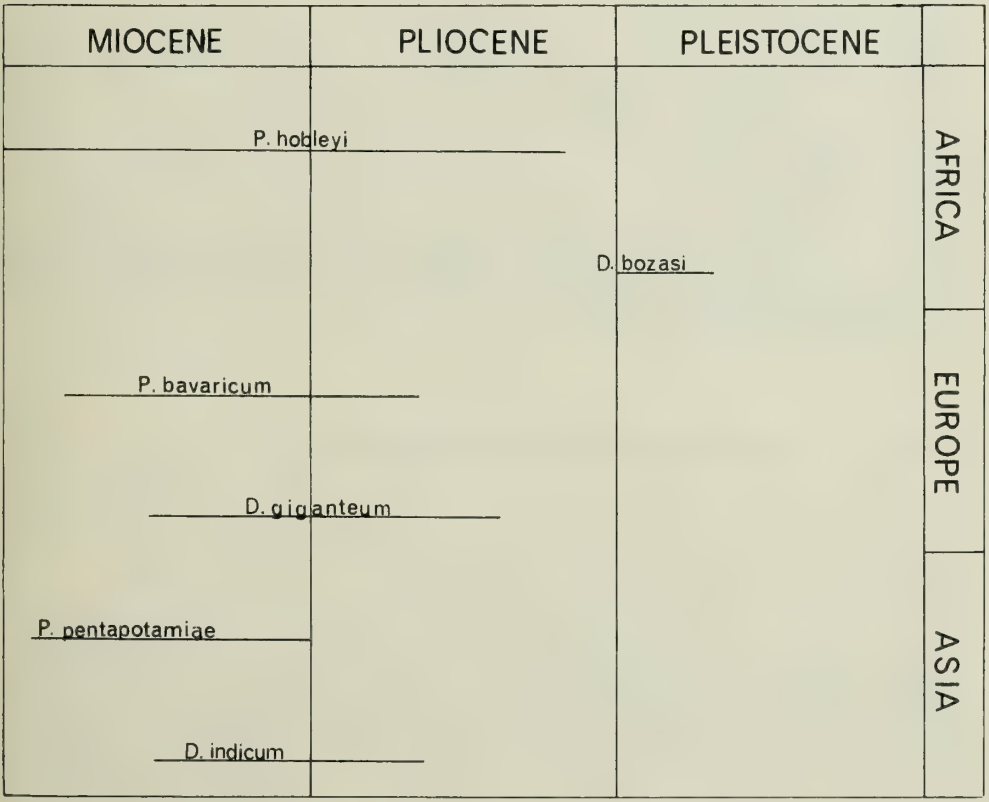


FIG. 2. Temporal and geographic distribution of deinotheriid taxa.

REMARKS. The family Deinotheriidae originated in Africa. The earliest and most primitive forms are from East African localities of early Miocene age. During the Burdigalian the early representatives of this family migrated into Asia and Europe. By the middle of the Miocene epoch, larger and more advanced representatives had appeared in Europe and Asia. The primitive and advanced forms coexisted until the end of the Miocene in Asia and the end of the Pontian in Europe. The more advanced forms lingered on until the middle Pliocene in Eurasia. Only the early and primitive form is known from the Neogene of Africa; a larger and more advanced form occurred in the Pleistocene but the two forms are not known to have coexisted.

Deinotheriid species have been commonly allocated to a single genus—*Deinotherium*—erected by Kaup in 1829. The species were defined upon geographic distribution and characters of the mandible and dentition. While the cheek teeth exhibit a great deal of variation in cusp morphology from specimen to specimen, these differences do not readily lend themselves to species differentiation, especially when the several species are interpreted as belonging to a single genus. Moreover the concept of a single deinothere genus does not adequately express the fundamental division of the family into an early and primitive group of species (*D. hobleyi*, *D. bavaricum* and *D. pentapotamiae*) and a later, more advanced group (*D. giganteum*, *D. indicum* and *D. bozasi*). The recent discoveries of deinotheriid skull and postcranial material, coupled with the re-examination of well documented specimens confirms that the two groups of deinotheres may be separated morphologically. It would appear therefore that division of the family into two genera is warranted. This idea was originally put forward by Ehik (1930) but has subsequently been ignored. On evidence currently available, however, Ehik's premise is substantiated. The two genera are defined below.

Genus **Deinotherium** Kaup, 1829

REVISED DIAGNOSIS. Large deinotheres. Dental formulae as for the family; tendency for the development of subsidiary styles on P^{3-4} and for simplification of the postmetaloph ornamentation of M^{2-3} when compared to *Prodeinotherium*. The skull rostrum not parallel to the mandibular symphysis and nearly horizontally aligned; rostral trough and external nares wide; preorbital swelling sited anteriorly on the rostrum; skull roof short and narrow at the temporal fossae; occiput slopes gently posteriorly; occipital condyles elevated above the level of the external auditory meatus; paroccipital processes very elongate. Postcranial skeleton with cursorial modifications to graviportal structure; scapular spine reduced with no acromion or metacromion; carpals and tarsals narrow with dolichopodous metapodials exhibiting functional tetradactyly.

Remarks. Most of the diagnostic characters of *Deinotherium* concern the skull and postcranial characters. The teeth, however, are the most commonly preserved remains. Teeth that may be attributed to *Deinotherium* are almost always larger than the equivalent teeth of *Prodeinotherium.* Both genera exhibit a tendency to increase in size through geologic time, and in Europe there is an overlap in absolute size of the cheek teeth of the two genera. This is due to the greater numbers and greater longevity of deinothere specimens from that continent, but at any one horizon the teeth of *Deinotherium* are always unmistakably larger than those of *Prodeinotherium.* On the basis of specimens examined and of those reported by Graf (1957), McInnes (1942) and Sahni & Tripathi (1957), the *minimum* parameters of *Deinotherium* teeth would appear to be as follows:

Tooth	Length (in mm)	Breadth (in mm)
P^3	63	55
P^4	59	62
M^1	71	64
M^2	70	74
M^3	70	74
P_3	51	43
P_4	61	48
M_1	74	54
M_2	73	63
M_3	75	65

These parameters agree well with those noted by Bergounioux & Crouzel (1962a) who also define parameters for the deciduous teeth.

Type species. *Deinotherium giganteum* Kaup, 1829 (including *D. gigantissimum* Stefanescu, 1897).

Other recognised species: *D. indicum* Falconer, 1845; *D. bozasi* Arambourg, 1934.

A detailed synonymy of *D. giganteum* was given by Graf (1957) and of *D. indicum* by Sahni & Tripathi (1957).

Genus ***Prodeinotherium*** Ehik, 1930

Revised diagnosis. Small deinotheres. Dental formulae as for the family; M^{2-3} with well defined postmetaloph ornamentation. Skull rostrum turned down parallel to the mandibular symphysis; rostral trough and external nares narrow; preorbital swelling close to orbit; external nares anteriorly sited and nasal bones with anterior median projection; skull roof relatively longer and wider than in *Deinotherium*; occiput more vertically inclined; occipital condyles sited more ventrally than in *Deinotherium* and level with the Frankfurt Plane; paroccipital processes short. Postcranial skeleton graviportally adapted; scapula with well defined spine and stout acromion and metacromion; tarsals and carpals narrow but not dolichopodous.

REMARKS. This genus was originally proposed by Ehik (1930) for a small species of deinothere from Kotyhaza, Hungary. The Kotyhaza specimens comprised a jaw, some teeth, and a few incomplete limb elements. These specimens were generally smaller than is normal in *D. bavaricum* but were subsequently attributed to this taxon without objection (Graf, 1957; Bergounioux & Crouzel, 1962a; etc.). I agree that the taxa *bavaricum* and *hungaricum* are probably conspecific but propose to allocate them to *Prodeinotherium*. Ehik's generic taxon is therefore resurrected to encompass the small, early and primitive species of deinothere from the Neogene of Africa and Eurasia. The slight change in spelling from *Prodinotherium* (Ehik, 1930) to *Prodeinotherium* is, in view of Kaup's spelling of the type genus of the family Deinotheriidae, considered to be a justifiee emendation according to the International Code of Zoological Nomenclature (Stoll *et al*, 1961) section 9, article 50, para graph (c).

Specimens that may be attributed to species of *Prodeinotherium* are observed to increase in size through geologic time. The *maximum* parameters for the permanent cheek teeth of *Prodeinotherium*, based on personal observation and data from Graf (1957), McInnes (1942), and Sahni & Tripathi (1957) are as follows:

Tooth	Length (in mm)	Breadth (in mm)
P^3	63	60
P^4	61	62
M^1	73	69
M^2	73	75
M^3	69	72
P_3	51	43
P_4	60	52
M_1	73	53
M_2	75	70
M_3	81	68

Similar figures are given by Bergounioux & Crouzel (1962a) who also define size limits for the deciduous teeth.

TYPE SPECIES. *Prodeinotherium bavaricum* (von Meyer), 1831.

OTHER RECOGNIZED SPECIES. *P. pentapotamiae* (Falconer), 1868; *P. hobleyi* (Andrews), 1911.

A detailed synonymy of *P. bavaricum* was given by Graf (1957) and of *P. pentapotamiae* by Sahni & Tripathi (1957).

TABLE 2

Comparison of *Prodeinotherium* and *Deinotherium*

	Prodeinotherium	*Deinotherium*
Skull.	rostrum ventrally flexed	rostrum almost straight
	rostrum narrow and deep	rostrum wide and shallow
	preorbital swelling close to external nares	preorbital swelling more anteriorly sited
	external nares almost as deep as wide	external nares much wider than deep
	external nares surmounted by median projection of nasals	no median projection of nasals
	orbit above P^3	orbit above P^4
	skull roof nearly flat and inclined anteriorly	skull roof shorter and narrower at the temporal fossae
	occiput steeply inclined	occiput gently inclined
	paroccipital processes longer than in elephantoids	paroccipital processes longer than in *Prodeinotherium*
	occipital condyles cut ventrally by Frankfurt Plane	occipital condyles elevated above Frankfurt Plane
Dentition.	P$^{3-4}$ usually lack mesostyles	P$^{3-4}$ often possess mesostyles
	M$^{2-3}$ with well developed postmetaloph ornamentation	M$^{2-3}$ with reduced postmetaloph ornamentation
	tusks nearly vertical	tusks longer and may be recurved beneath symphysis
Skeleton.	scapula—stout spine, metacromion and acromion; supraspinous fossa well developed	scapula—reduced spine and no metacromion or acromion; supraspinous fossa greatly reduced
	humerus—lateral epicondyle tapers proximally	humerus—lateral epicondyle does not taper proximally
	radius—medial half of head larger than lateral half; distal epiphysis more massive than in *Mastodon angustidens*	radius—medial half of head correspondingly larger; distal epiphysis more massive than in *Prodeinotherium*
	lunar—radial facet covers most of proximal surface; magnum facet is concavo-convex	lunar—radial facet extends less far posteriorly; magnum facet almost flat
	cuneiform—posterolateral process of similar length to that of *Elephas* but does not articulate with unciform; unciform facet is concavo-convex	cuneiform—posteriolateral process is relatively longer and more ventrally inclined than in *Prodeinotherium*; unciform facet is biconcave
	unciform—cuneiform facet roughly triangular; largest distal facet is for McV	unciform—cuneiform facet extends farther posterolaterally and distally, and tapers more abruptly posteriorly; largest distal facet is for McIV
	magnum—proximal surface has large posteromedial projection	magnum—posteriomedial projection is less pronounced
	metacarpals—laterally compressed but of similar size to *Mastodon angustidens*	metacarpals—more compressed laterally and distinctly more elongate than in *Prodeinotherium*
	manus more plantigrade	manus more digitigrade
	femur—similar length to *Elephas maximus*	femur—proportionately 30% shorter than in *E. maximus*
	astragalus—tibial facet equant and convex; prominent posteromedial process	astragalus—tibial facet equant but nearly flat posteromedial process more reduced than in *Prodeinotherium*

Teeth are the most common deinothere remains, but although there is a great deal of variation in minor topographic features on the cheek teeth the basic tooth morphology is conservative throughout the known history of the group. Indeed, when only a single genus—*Deinotherium*—was accepted, tooth morphology was of far less importance for specific differentiation than absolute size of the teeth or geographic distribution of the specimens. In effect only two distinct species could be recognized—*D. giganteum* and *D. bavaricum*. However, with these two taxa separated by generic rank, tooth morphology assumes greater diagnostic importance. It is entirely possible that detailed revision of known material will furnish evidence for distinguishing different lineages within the two genera incorporating variations in cheek tooth morphology. Such a revision is, however, beyond the scope of this paper.

Only two deinothere species are currently recognized from fossil mammal sites in Africa—*Prodeinotherium hobleyi* of the Neogene and *Deinotherium bozasi* of the Quaternary. The Gebel Zelten deinothere teeth are more advanced than specimens of *P. hobleyi* from the earliest Miocene of East Africa but more primitive than those from Ngorora (Pliocene) in Kenya. The observed differences are insufficient at present to warrant the erection of a separate taxon for the Libyan material.

Prodeinotherium hobleyi (Andrews), 1911

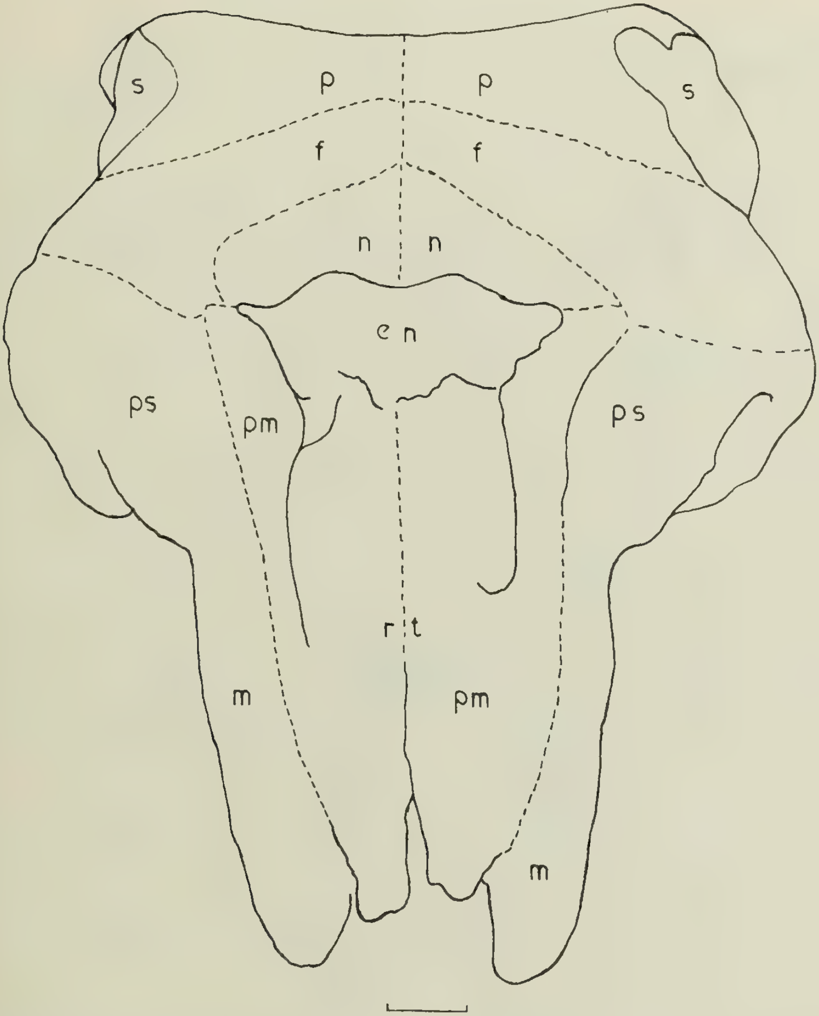
1911 *Deinotherium hobleyi* Andrews: 943.
1919 *Deinotherium cuvieri* Kaup; Brives: 90.
1957 *Deinotherium bavaricum* v Meyer; Graf: 152.
1967 *Deinotherium cuvieri* Kaup; Savage: 263.

Skull

(Text-figs 3–6; Plates 1–3)

Material referred. 6404 : 14, fragmentary adult skull with only the dentition, right premaxilla, left jugal and occipital condyles well preserved; 6404 : 44, complete but slightly distorted immature skull; M.26665, virtually complete skull but with zygomatic arches, squamosal, auditory and pterygoid regions poorly preserved; 6418 : 4 and 6418 : 19, incomplete and uncollected skulls.

Description. The skull of *Prodeinotherium hobleyi* from Gebel Zelten is elongate and low, the length of the cranium being twice that of the rostrum. The skull is characterized by a relatively flat skull roof which ascends gently to the lambdoidal crest, a small orbit that is open posteriorly, a broad and downturned rostrum that is surmounted by massive preorbital swellings, high occipital condyles, and a backwards sloping occipital region. The rostrum is appreciably narrower than in *Deinotherium giganteum* and is excavated to form a deep rostral trough anterior to the external nares. The occipital region is very wide owing to the well developed lateral wings of the squamosal bones. Much of the skull is formed from cancellous bone, and where the surface bone has been eroded diplöe similar to those of elephantoid skulls may be detected.



Key to letters used in text-figures 3, 4, 5 & 6.
b = auditory bulla
en = external nares
f = frontal
fo = foramen ovale
fr = foramen rotundum
ga = glenoid articulation surface
in = internal nares
io = infraorbital foramen
lc = lamboidal crest
ls = lateral wing of squamosal
m = maxilla
n = nasal
ns = nasal sinus
o = orbit
oc = occipital condyle
p = parietal
pf = posterior palatine foramen
pgf = postglenoid fossa
plf = posterior lacerate foramen
pm = premaxilla
po = postorbital process of frontal
pp = paroccipital process
ps = preorbital swelling of maxilla
pt = pterygoid process
rt = rostral trough
s = squamosal
tf = temporal fossa
zm = zygomatic process of maxilla
zs = zygomatic process of squamosal

FIG. 3. *Prodeinotherium hobleyi* skull, anterior view. Scale = 5 cm.

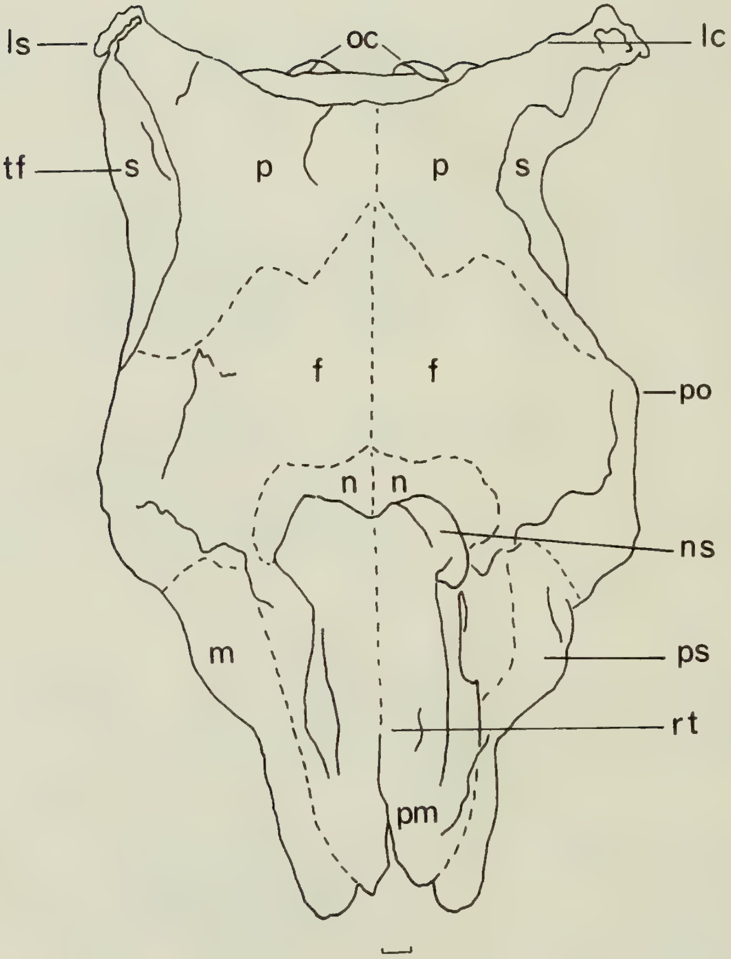

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FIG. 4. *Prodeinotherium hobleyi* skull, dorsal view. Scale = 5 cm.

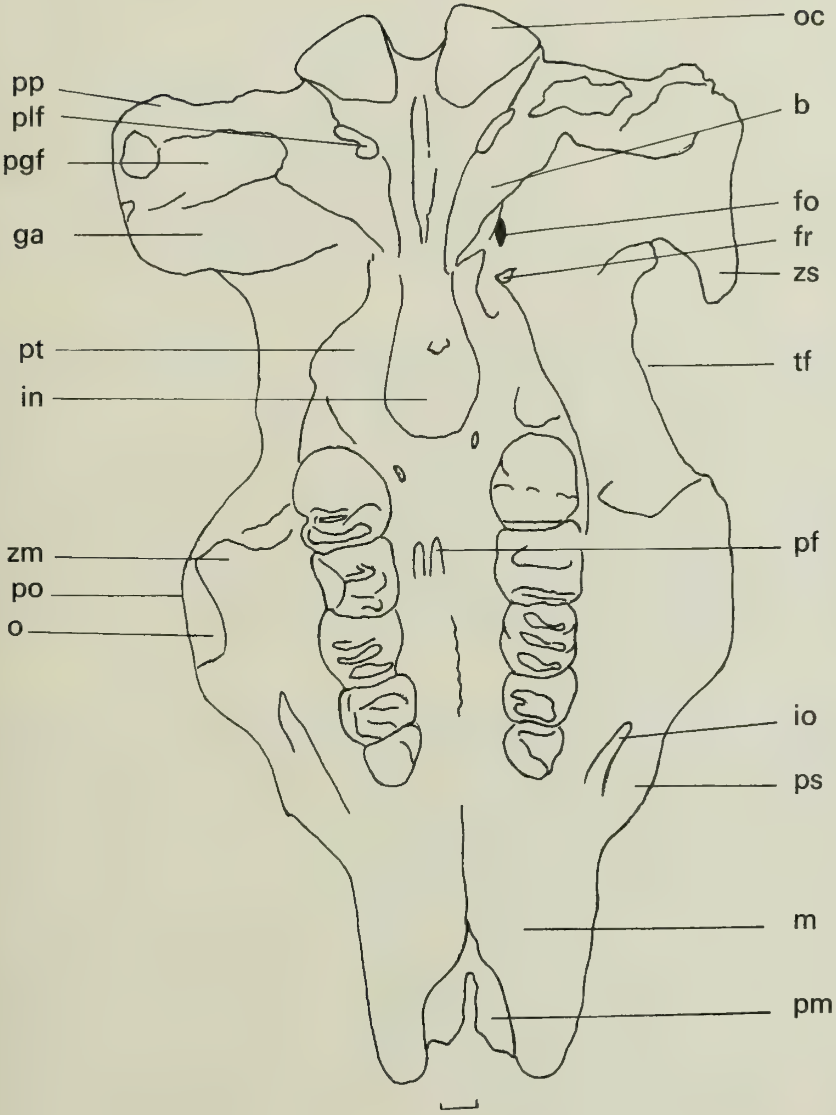
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FIG. 5. *Prodeinotherium hobleyi* skull, ventral view. Scale = 5 cm.

Premaxilla. The dorsal surface of the deep rostral trough (text-figs 4, 5) anterior to the external nares is lined by the premaxillae. The anterior portion of the premaxilla forms a small flange projecting anteriorly from the upstanding rugose walls of the rostral trough (Pl. 1a). The premaxillary-maxillary suture extends from the lateral edge of this flange along the medial edge of the wall of the rostral trough until it meets the anterior wing of the nasal (text-figs 3, 4). The suture has completely fused in skull M.26665 but the premaxillary-maxillary contact is denoted by the junction of smooth bone, typical of the medial walls and floor of the trough, with the rugose bone of the lateral walls and dorsal surface. The suture is still visible in skull 6404 : 44. The posterior limit of the premaxilla beneath the external nares is not clear owing to the fusion of sutures in M.26665 and the cracked nature of the bone in 6404 : 44. Perhaps the limit is marked by the anterior edge of the cavernous nasal sinus (text-fig. 4, Pl. 1b) that occurs on either side of the external nares.

Viewed from the dorsal aspect, each premaxilla is roughly triangular with the posterior edge of the bone forming the shortest side. In transverse section the distal part of the premaxilla is L-shaped, the ascending arm lining the medial wall of the rostral trough while the body forms the floor. Medial to the preorbital swelling of the maxilla (text-figs 3, 4, 5; Pls. 1–2), the ascending process of the premaxilla bulges medially in front of the nasal sinus, and here the surface of the bone is curved sigmoidally. The facial process of the premaxilla ascends to contact both the nasal and the anteriormost prolongation of the frontal bone (text-figs 3, 4), thereby excluding the maxilla from contact with the nasal. Ventrally the premaxilla is visible only at the anterior third of the rostrum where the premaxillary flanges appear above the diverging tips of the maxillae (text-fig. 5; Pl. 3b). The flanges of the premaxillae converge ventrally.

Maxilla. This is the largest bone of the facial region, extending from the dental alveoli up to the level of the external nares, and from the anterior tip of the rostrum to behind the dentition. The facial process of the maxilla is contiguous with the frontal, lacrimal and premaxilla. It continues forwards and downwards from the orbit as the external wall of the rostral trough. Just anterior to the frontal-maxillary suture the dorsal and dorsolateral parts of the rostral walls are swollen in skull M.26665 to form a massive preorbital swelling. In 6404 : 44 the swelling is less pronounced but this portion of the maxilla is considerably elevated above the remainder of the dorsal rim of the rostral trough. The infraorbital foramen (Pl. 2a and b) is large and the anterior opening lies above the anterior edge of the third premolar. In skull M.26665 two deep grooves extend anteriorly from the infraorbital foramen. One runs for a short distance down the lateral surface of the rostrum; the other extends parallel to the dentition to terminate on the dorsal surface of the rostral trough immediately in front of the preorbital swelling. These grooves mark the proboscideal branches of cranial nerves V and VII. In skull 6404 : 44 only the former groove is well developed. The jugal process of the maxilla is stout, expanding posteriorly to define the posteroventral limit of the orbit (Pl. 2a). The posterior opening of the infraorbital canal is sited above the base of the jugal process of the maxilla and beneath the postorbital process of the frontal (Pl. 2b).

In ventral aspect the maxillae diverge behind the anterior third of the rostrum, revealing the margins of the premaxilla. Behind the anterior third of the rostrum the intermaxillary suture extends posteriorly down the midline of the palate as a cristiform ridge (Pl. 3b). The maxillary-palatine suture is fused in skull M.26665 but is presumed to have been level with the posterior root of the second molar and to have incorporated the paired posterior palatine foramina. Shallow grooves extend anteriorly from these foramina until level with the fourth premolars. The lingual border of the alveolar region is continued forward from the anterior root of the premolar as a broad, rounded ridge, converging on its fellow towards the tip of the rostrum. On the medial side of this ridge a very weak crest extends anteriorly to meet the ventral exposed portion of the premaxilla. The plate is vaulted in the vicinity of the premolars and narrows as it continues forwards beneath the rostrum. In the region of the molars the palate is convex.

Nasal. In skull M.26665 the nasal-frontal suture is fused but there is a pronounced break of slope some 7 cms behind the external nares that probably indicates the junction of these bones. The surface of the bone immediately above and behind the external nares is much smoother than the adjoining bone. In 6404 : 44 the lateral wing of the nasal extends laterally until level with the front of the orbit and the suture with the premaxilla is well defined. In dorsal plan the nasals are crescentic (text-fig. 4). In M.26665 the nasals continue anteriorly at the intranasal suture to form a well developed median projection (Pl. 1a and b) though this is less well developed than that of the extant elephants. In 6404 : 44 the anterior portion of the intra-nasal suture is marked by an indentation rather than by a projection; this is attributed to the relative immaturity of the specimen. Apparently the nasal bones do not contribute to the cavernous nasal sinuses on either side of the external nares.

Lacrimal. Due to fusion of the sutures and to incomplete preservation the lacrimal is not well delineated in skull M.26665 but in 6404 : 44 the lacrimal is seen to form the anteroventral quadrant of the rim of the orbit. The lacrimal bone is triangular with the base of the triangle elevated a short distance above the infraorbital canal. From the centre of the ventral half of the bone a lacrimal foramen opens into a lacrimal canal that passes outwards to the anteroventral rim of the orbit. Above the lacrimal foramen is a large traction epiphysis. The lacrimal is contiguous only with the frontal and maxilla and does not form part of the infraorbital swelling of the maxilla (cf. Andrews, 1921; 530).

Jugal. This bone is missing from skull M.26665 but is known from 6404 : 44 and from the incomplete skull 6404 : 14. The jugal joins the zygomatic process of the maxilla at the posteroventral edge of the orbit, at which point the zygomatic process of the maxilla attains its greatest height. From the vertical jugal-maxillary suture the jugal increases in height posteriorly while simultaneously becoming flattened from triangular to oval in transverse section. The posterior portion of the jugal is overlapped by the zygomatic process of the squamosal. The posterior end of the jugal forms a smooth convex curve and gives off a small conical process from the posterior ventral surface. A jugal from skull 6404 : 44 is less massive and lacks the conical process on the posterior ventral surface.

Palatine. This is fused to the palatine process of the maxilla level with the posterior root of M^2 and extends for some distance behind M^3. The palatine is pierced by two asymmetrically placed posterior palatine foramina. In M.26665 the anteriormost part of the palatonarial border is sited some way behind M^3 and is gently curved with the lateral, more posterior, portions missing. The internal narial opening is almost circular.

Vomer. The vomer extends back behind the level of the anterior part of the palatonarial border and forms a V-shaped crest along the roof of the internal nares. Immediately above the posterior end of the vomer a small chip of bone is missing in skull M.26665 thus revealing part of the cavernous ethmoidal fossa.

Frontal. In M.26665 the frontal bones occupy just over half of the skull roof (text-fig. 4). The nasal-frontal suture is fused but the anterior edge of the frontals may be determined as above. Part of the frontal-parietal suture is revealed in the centre of the skull roof of M.26665 as a sinuous interdigitating groove but this cannot be traced laterally. The frontals are slightly domed convexly in the midline and over the large postorbital processes. There are no supratemporal ridges. Both the frontal and parietal portions of the skull roof extend ventrally to contribute to the temporal fossa. The postorbital processes of the frontals (text-fig. 4) are blunt protruberances from each of which a ridge descends ventrally and posteriorly to continue as the free end of the alisphenoid. In front of these processes the frontals demarcate the upper rim of the orbit.

Parietal. The parietal bones form the posterior part of the skull roof. They increase in width anteriorly from the lambdoidal crest. The lambdoidal crest forms the most elevated portion of the skull roof and strongly delineates the latter from the occipital region. The dorsal surface of the parietals is slightly concave in transverse section and there is no sagittal crest.

Fusion of the sutures on the posterior half of the cranium makes the boundary of the parietals indistinct. Even in the immature skull (6404 : 44) the junctions of the parietals, squamosals, alisphenoids and frontals are not clear. Beneath the sharply delineated rim of the temporal fossa the bone in M.26665 is sculpted by deep and wide grooves denoting the point of attachment of the temporal muscle. Ventral to the sculpted surface the bone is much cracked and broken. In 6404 : 44 the walls of the temporal fossae are better preserved but the bone shows no temporal muscle scars. No trace of an interparietal may be detected.

Supraoccipital. This contributes to the central and dorsal regions of the occiput (Pl. 3a) and is concave both sagittally and transversely. The perimeter of this bone is fused but it must have been roughly triangular; whether or not it formed the dorsal border of the foramen magnum cannot be determined. The dorsal edge contributes to the posterior side of the central portion of the lambdoidal crest. The lateral junction with the squamosal may be indicated by a pronounced ridge that extends from the paroccipital process to the lamboidal crest. The supraoccipital is excavated in the midline by two deep triangular pits that form fossae for the nuchal ligament. The dorsal edge of the nuchal fossa lies some 5 cms below the lambdoidal crest; the ventral edge some 8 cms above the foramen magnum. As in elephantoid skulls, the two halves of the nuchal fossa are separated by a narrow ridge of bone. The floor of each pit is comprised of sculpted bone, as is that region between the top of the nuchal fossa and the lambdoidal crest.

Exoccipital. The paired exoccipital bones form the ventrolateral regions of the occiput and support very large and prominent occipital condyles. From the dorsolateral edge of the nuchal fossa of skull M.26665 a prominent crest curves ventrally and laterally to terminate on the lateral edge of the paroccipital process. This ridge is interpreted as separating the exoccipital from the lateral wing of the squamosal and is continuous with the lateral limit of the supraoccipital. The condyles are triangular and converge as they taper ventrally. The condyles are limited ventrally by a deep groove (the condyloid fossa of Palmer, 1924) that is also present, though less prominent, on the dorsal edge. The condyles are most elevated from the rest of the exoccipital bone at their anteromedial edge at which point they protrude almost at right angles from the plane of the occiput. The paroccipital processes are incomplete on M.26665 but on 6404 : 44 are seen to extend for some distance below the base of the occipital condyles, merging laterally with the ventral edge of the lateral wing of the squamosal.

Basioccipital. Fusion of the sutures and incomplete preservation prevents delineation of the periphery of this bone in M.26665. The basioccipital descends steeply from the foramen magnum and becomes progressively more narrow anteriorly (text-fig. 5; Pl. 3b). The posterior part is deeply notched by the foramen magnum and extends laterally to the medial edges of the occipital condyles. Anteriorly and ventrally the body is keeled. The anteroventral junction with the basisphenoid is probably level with the glenoid articulation surface. The basisphenoid passes uninterruptedly from the basioccipital but the keel becomes less pronounced anteriorly and disappears before reaching the internal narial opening.

The basicranium of 6404 : 44 has been distorted by crushing and the ventral surface is now parallel with the left lateral side. Slightly anterior to, and on either side of, the notch excavated by the foramen magnum is a large boss. This probably served for the insertion of the rectus anticus muscles. The right boss is level with, but somewhat below, the paroccipital process. The left boss is less well preserved. From this point the basioccipital narrows appreciably as it continues anteriorly. Some 5 cms in front of the anterior edge of the foramen magnum a pronounced keel extends down the midline. This keel extends for at least 9 cms until level with the eustachian opening of the auditory bulla but in front of this point the bone is too badly displaced to allow further observation of the keel. On either side of the posterior end of the keel are excavated large fossae for insertion of the rectus anticus major muscles. An elongate notch, the posterior lacerate foramen, is sited anterior to the paroccipital process and lateral to the basioccipital at the posterior end of the keel.

Sphenoid. The junctions of the various component parts of this bone with each other and with contiguous elements are for the most part indistinct. The anterior boundary of the alisphenoid forms part of the prominent cristiform outer wall of a deep groove that extends from the pterygoid process to the postorbital process of the frontal. The optic foramen, that probably perforated the orbitosphenoid, lies some distance above and anterior to the slit-like anterior lacerate foramen, and the orbitosphenoid-alisphenoid suture undoubtedly lay somewhere between the two. Both foramina lie in a deep groove beneath the alisphenoid-frontal ridge. From the optic foramen a shallow groove extends forwards to the orbit, marking the course of the optic nerve. The foramen rotundum lies posterior to the anterior lacerate foramen and opens from the alisphenoid flap into a large alisphenoid canal. The mandibular branch of the fifth cranial nerve emerged from the posterior opening of the alisphenoid canal while the facial and maxillary branches emerged from the anterior opening. The position of the maxillary branch is marked by a deep groove, partly covered by a flap of bone, that extends towards the pterygoid process. In skull M.26665 this groove extends almost vertically (Pls. 2a and b) but in 6404 : 44 it passes anteriorly at an angle of 45°. Behind the posterior exit of the alisphenoid canal, and above the anterior portion of the auditory bulla, is a large foramen ovale (text-fig. 6).

The pterygoid region is very poorly preserved in skull M.26665. Ventrally and medially it passes uninterruptedly into the presphenoid and posteriorly into the alisphenoid. Nearly all of the ventral part that, together with the palatine, forms the lateral border of the internal nares is missing. The posterior surface of the pterygoid forms a smooth crest that passes laterally to the anterior tip of the petrosal. This region is also poorly preserved in skull 6404 : 44.

Squamosal. This is one of the largest bones of the skull and forms the posteroventral wall of the temporal fossa. It is only poorly preserved in M.26665 and in many places the surface bone is missing to reveal diplöe beneath. The squamosal continues anteriorly and laterally from the supraoccipital to project as a vast lateral wing forming the widest part of the skull (text-fig. 4; Pl. 1b). The external edge of this wing passes uninterruptedly from the lambdoidal crest into the paroccipital process of the exoccipital. In lateral aspect the junction of the squamosal with both the alisphenoid and the parietal is indistinct. The zygomatic process of the squamosal is less stout than that of the maxilla, being almost quadrate in transverse section near the point of origin but becoming more slender as it extends forward

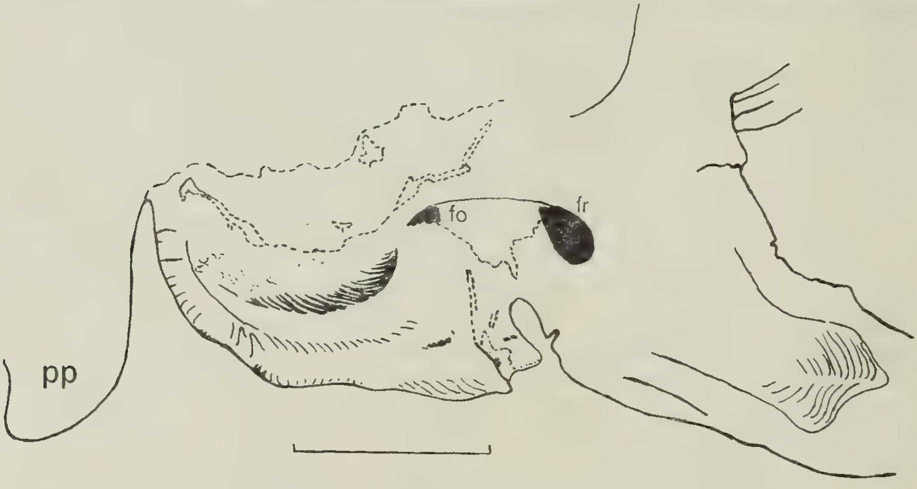

FIG. 6. *Prodeinotherium hobleyi* right auditory bulla. Scale = 5 cm.

to overlap the jugal. The auditory meatus opens onto the external surface of the lateral wing immediately posterior to, and slightly above, the zygomatic process. In M.26665 this region is poorly preserved but in 6404 : 44 the passage of the meatus is clearly seen. The passage of the meatus is gently inclined medially. The glenoid articulation surface is convex and elongate transversely. There is no postglenoid process and behind the glenoid surface there is a shallow transverse channel forming the floor of the auditory meatus as in *Elephas*.

Tympanic bulla. The tympanic bullae are incompletely preserved in M.26665 but are seen to be relatively larger than in the skull of *D. giganteum* from Eppeslheim, Germany. Much of the surface bone on the Gebel Zelten specimen is missing and sufficient detail is preserved to show only the eustachian opening below and behind the foramen ovale. In skull 6404 : 44 both bullae are present but the left bulla is incomplete and crushed and the right bulla (text-fig. 6) is incomplete. The bullae are bounded medially by the basioccipital and basisphenoid (contributing in part to the posterior lacerate foramen), posteriorly by the paroccipital process, and dorsally by the squamosal and alisphenoid. The bulla projects ventrolaterally as a semicircle of bone. In dorsal aspect it may be divided into two unequal portions—a posterior concave surface and an anterior (slightly larger) convex area. The regions are separated by a ridge that runs posteriorly and laterally from the foramen ovale to merge with the lateral perimeter level with the posterior lacerate foramen. The concave area thus enclosed presents an irregular surface pitted with numerous small foramina. The anterior portion of the dorsal surface is convex and consists mainly of smooth bone although it is pierced by several small foramina and canals near the anterolateral edge. The eustachian opening occurs at the anteromedial tip.

On skull 6404 : 44 the ventral surface of both bullae is incomplete but sufficient bone is preserved to permit a composite description. The ventral surface is divided sagittally into two unequal portions by a crest that extends from the paroccipital process to the anterolateral margin of the bulla. The portion of the bulla lateral to the crest is the smaller. The ridge is most pronounced posteriorly where it separates the posterior lacerate foramen from the large stylomastoid foramen, and becomes progressively less distinct anteriorly. The bone anterior to the stylomastoid foramen and lateral to the ridge is concave transversely and heavily sculpted. This part of the bulla is equivalent to the tympanohyal pit. Medial to the crest the surface of the bulla is smooth but cut by transverse shallow grooves. This portion of the left bulla is crushed and fragmented; on the right bulla the surface bone is missing from the anteromedial region to reveal the cavernous tympanum. In comparison with that of the extant elephants, the tympanic bulla of *Prodeinotherium* is less elongate sagittally and wider transversely with a larger stylomastoid foramen.

OTHER DEINOTHERIID SKULLS. *Prodeinotherium pentapotamiae.* An incomplete skull of *P. pentapotamiae* was collected in 1912 by Pilgrim from the Lower Chinji Sandstone, four miles from Chinji in the Salt Range of India. Two portions of the skull are preserved—a palate with cheek teeth (I.M. A.460) and a basicranium (I.M. A.461). These are of similar size to those of the Gebel Zelten skulls and were described by Palmer (1924). The skull foramina that Palmer identified are sited similarly to those of the Gebel Zelten skulls. Only the base of the vertical tapering pillar that Palmer identified as the hyoid is still preserved but the basal tympanohyal portion would have fitted well into the elongate and narrow tympanohyal pit anterior to the stylomastoid foramen in Gebel Zelten skull 6404 : 44. Unlike Palmer, I do not believe that the right paroccipital process of the Indian skull can be far from its original position. Palmer had correctly identified the tympanic bullae, unlike Andrews (1921), but these are now only poorly preserved on the Indian specimen.

Eppelsheim skull. The skull of *Deinotherium giganteum* from Eppelsheim, Germany, was originally described by Klipstein and Kaup (1836) and the most recent description of this specimen was given by Andrews (1921). In the light of the information provided by the Gebel Zelten *Prodeinotherium* material it is now necessary to revise some of Andrews' interpretations of the Epplesheim specimen. For example, on page 527 Andrews remarks:

> ' . . . de Blainville suggests that possibly the occipital surface had been crushed down towards the floor of the skull. Careful examination of the specimen, however, does not seem to support this idea and it seems probable that . . . it represents the condition of the living animal.'

TABLE 3

Prodeinotherium hobleyi skull measurements

Parameter	M.26665	6404 : 44
Total length of skull	94	73
Width anterior tip of rostrum	13·6	10·1
Length rostrum to external nares	42	34
Width skull at external nares	53	38
Width rostral trough at external nares	17·8	11·8
Length external nares to lambdoidal crest	40	31
Minimum width skull roof	42	28
Width lambdoidal crest	59·6	35
Height foramen magnum to lambdoidal crest	25·4	—
Height nuchal fossa	12·3	12·6
Width nuchal fossa	15·9	11·1
Width occipital condyles	27·2	—
Height foramen magnum	6·4	—
Width foramen magnum	7·7	—
Height molar alveoli to lambdoidal crest	41·9	31*
Width glenoid condyles	13·7	—
Length palatonarial border to rostrum tip	56	84
Width palate at P^3	7·3	—
Width palate at M^1	10	—
Width palate at M^3	8·3	—

The cracked condition of the bone and asymmetry of the left and right lateral wings of the squamosals reveal that the Eppelsheim skull has undergone at least a modicum of postmortem distortion, either during burial or after excavation. Differences between the cast of the ventral side and the specimen itself indicate that some post-excavation restoration has been necessary. Indeed, much of the squamosal region is now plaster of paris. Certain anomalous features of the Eppelsheim skull are discussed later and indicate that restoration has not always been skilful or accurate.

On page 528 Andrews stated 'In *Deinotherium* no development of cellular bone seems to have taken place.' This is clearly wrong. In the Eppelsheim skull, as in the Gebel Zelten skulls, portions of the surface bone are missing to reveal cellular bone beneath. This phenomenon was noted in de Blainville's earlier description of the skull (de Blainville, 1837) and was confirmed by Palmer (1924) in his description of the skull of *P. pentapotamiae*. Skull 6404 : 14 from Gebel Zelten was unfortunately shattered in transit to Bristol but the fragments salvaged leave no doubt that much of the skull was composed of cellular bone.

On page 529 Andrews noted that 'in front of the orbit the maxilla forms a great mass of bone terminating in a rugose, somewhat concave surface for the attachment of muscles'. These concavities are preservation anomalies and not original morphological features. That on the left side is much smaller than the right concavity. In corollary the preorbital swellings of the Eppelsheim skull are unequal, that on the left being much larger. During restoration a large piece of bone has been cemented on to the anterior part of the left swelling thus increasing its total size. This piece of bone is the same length as the concavity on the right side and, if it were to be transferred there, the preorbital swellings would be (a) symmetrical, (b) of similar size and (c) convex.

Further, on page 530, Andrews declared:

> 'The point of union of the premaxilla (with the maxilla) is probably marked by the sudden narrowing of the snout about 40 cms in front of the orbit.'

This sudden narrowing marks the anterior termination of the preorbital swelling. The 'suture' to which Andrews refers in the next sentence occurs on both the dorsal and ventral surface of the rostrum and bisects both the premaxilla and maxilla. It appears likely that the anterior part of the rostrum was once detached and the 'suture' marks the point of breakage. The actual suture between the premaxilla and maxilla is well seen on Gebel Zelten skull 6404 : 44 and there is no reason to believe that the geometry of these bones differed appreciably on the Epplesheim skull.

The anterodorsal surface of the external nares appears to be complete and is similar in morphology to the equivalent portion of a skull fragment of *Deinotherium giganteum* from Palencia, Spain. There is no anterior median process in contrast to the condition in Gebel Zelten skull M.26665. The lacrimal bone cannot be observed in the Eppelsheim skull but was more likely to have occupied a similar position to that in 6404 : 44 than to have formed part of the preorbital swelling (cf. Andrews, 1921 : 530), especially as the latter feature is found farther forward than in the Gebel Zelten skulls. The 'irregularly arranged pits' at the anterior end of the premaxilla (Andrews, 1921 : 531) are not, as Andrews suggested, rudimentary tusk alveoli but diplöe revealed by erosion of the external surface of the bone at this point.

Any comparison made between the occipital regions of the Eppelsheim and Gebel Zelten skulls is liable to be suspect for the roof of the Eppelsheim specimen is incomplete posteriorly. The lambdoidal crest appears to be missing and much of the bone between the foramen magnum and the lambdoidal crest is either absent or distorted (cf. Andrews, 1921 : 527). The shape of the occipital surface of the Eppelsheim skull appears to be more oval than in the Gebel Zelten skulls and the nuchal fossa is shaped differently. The nuchal fossa of the Eppelsheim skull may be divided into two portions—an anterior deep and wide oval pit (long axis transversely orientated) and a posterior triangular trough that is shallower and tapers ventrally. The latter trough may be all that remains of the true nuchal fossa on the Eppelsheim skull.

The 'large post-tympanic flanges' (Andrews, 1921 : 527) are equivalent to the paroccipital processes of other mammals and are, as Andrews described, formed partly of the exoccipitals and partly of the squamosals. The paroccipital processes are smaller in the Gebel Zelten skulls. The 'tongue-like process of bone' (Andrews, 1921 : 527) that is attached to the left paroccipital process was incorrectly identified by Andrews as the paroccipital process itself. This piece of bone is seen only on the left side of the skull and is more likely to represent part of the hyoid bone (cf. Palmer, 1924 : 4). The large convex bulbs that Andrews (1921 : 530; fig. 3) interpreted as tympanic bullae are seen also on Gebel Zelten skull 6404 : 44 where I have interpreted them as bosses for the insertion of the rectus anticus muscles. The tympanic bullae of the Epplesheim skull are more likely to be represented by a strong crest of bone that terminates posteriorly at the hyoid and extends forward apparently to merge with the pterygoid flange. A petrosal of *D. giganteum* was described by Claudius (1865) but the original specimen is now lost and the accuracy of its identification must be regarded as questionable (pers. comm. H. Tobein).

Munich skull. Stromer (1938) described the remains of a skull, mandible and partial skeleton of *D. giganteum* from the Sarmatian Flinzsande of Munich. Unfortunately all except the cast of the palate were subsequently destroyed and only Stromer's description and diagrams are now available for study. The skull was originally incomplete, lacking the lower part of the occiput, the basicranium, the ventral walls of the temporal fossa and part of the skull roof. However the fragments that were collected are of importance in that they are less distorted than some portions of the Eppelsheim skull.

The rostral flanges of the premaxilla and maxilla are separated in the midline as in the Eppelsheim skull, and are flexed at a similar angle, i.e. less steeply than *Prodeinotherium.* The preorbital swellings were either not developed or have not been preserved. The surface of the skull roof was relatively flat and, as restored by Stromer, may have been more horizontal posteriorly than in the Gebel Zelten skulls. Only the upper portion of the occiput was preserved and was described as strongly inclined posteriorly, though this cannot be detected from the illustrations given by Stromer. The lateral wing of the squamosal was more vertically aligned than in the Eppelsheim skull and strongly resembles that of *Prodeinotherium*, indicating that the Eppelsheim skull was badly deformed in this region.

Palencia skull. The skull roof and palate of *D. giganteum* from Castrillo de Villavega, Palencia, Spain, is housed in the Madrid Natural History Museum. The nasal bones are represented but are incompletely preserved on the right side. They surmount an external narial opening that is greatly compressed dorsoventrally. The lateral sinuses, which are large on the Gebel Zelten *Prodeinotherium* skulls, are much less prominent in the Palencia specimen. The nasal-frontal suture is fused but the nasals are demarcated as a flat surface projecting anteriorly at an angle from the remainder of the skull roof. The intra-nasal suture is fused and there is no anterior median projection of the nasals over the external nares. The skull roof forms a hollow behind the posterior edge of the nasals and in front of the lambdoidal crest. The lambdoidal crest is incomplete on the right side but on the left extends down the lateral wing of the squamosal to contribute to the widest part of the skull. The postorbital process of the frontal is very large and the anterior portion is located in front of the external nares. Behind the postorbital process the lateral surface of the temporal fossa is strongly delineated from the skull roof, the angle between the two surfaces being in the order of 45°.

Only the dorsal edge of the occipital surface is preserved and this had been incompletely prepared. It is not therefore possible to determine at present whether the occiput was inclined as in the Eppelsheim skull or the Gebel Zelten specimens. The nuchal fossa is incomplete. The shape indicated by the upper part of the fossa is approximately triangular and the dorsal edge of the fossa sited only some 5 cms below the lambdoidal crest. Although the orbit is not represented on this specimen the position of the postorbital processes suggests that the orbit was sited in advance of the external nares in contrast to the situation in the Gebel Zelten specimens.

DISCUSSION. Comparison of the skulls of *Prodeinotherium* and *Deinotherium*, as represented by the Gebel Zelten, Eppelsheim and Palencia specimens, yields evidence of both positive and negative allometric changes. Using the overall skull length as a basis for comparison, parameters that remain the same in both genera are skull width at the external nares, width at the lambdoid crest, and length of the rostrum. The only major increase in width is in the rostral trough of *Deinotherium* and this is exhibited in both the Palencia and Eppelsheim skulls. In both these skulls the external nares are also sited farther posteriorly than in *Prodeinotherium* and are considerably less deep than wide—converging on the elephantoids in both position and shape. The length and width of the skull roof are proportionately smaller in *Deinotherium* than in *Prodeinotherium*. The facial/cranial region ratio remains constant and the decrease in skull roof length in *Deinotherium* is directly proportional to the increase in area of the occipital region due to the anterior inclination of the latter. The shorter skull roof of *Deinotherium* is also correspondingly narrower. This is a compensatory feature to permit a large area of origin of the temporal muscles despite a shorter skull roof.

The majority of the differences between the cranial morphology of *Deinotherium* and *Prodeinotherium* involve only relatively minor allometric changes and some of these are foreshadowed by the differences between the immature (6404 : 44) and mature (M.26665) *Prodeinotherium* skulls. Thus the rostrum is more steeply downturned in M.26665 than in *Deinotherium* and the rostral flexure of 6404 : 44 is even more pronounced. Decrease in rostrum curvature in *Deinotherium*, together with increase of rostral width and retraction of the external nares, suggests the development of a more powerful and effective proboscis in the later genus. The length measurements of 6404 : 44 and M.26665 are very similar but the skull width parameters are relatively smaller in the immature specimen.

In *Deinotherium* the elevation of the occipital condyles, elongation of the paroccipital processes and increase in inclination of the occiput are associated with functional changes enhancing the downward movement of the head (and thereby the tusks). The greater inclination of the occiput has contributed to a decrease in the length of the skull roof, although this is also affected by the more posterior siting of the external nares. The shorter skull roof limits the potential area of attachment of the temporal muscles but this is compensated for by excavation of the temporal fossa and decreased width of the skull roof. In this way major changes in cranial morphology in the Deinotheriidae are associated with proboscis development and with increase in potential movement of the skull on the neck, both factors suggesting changes in feeding methods and habits.

TABLE 4

Deinotherium skull measurements

Parameter	Eppelsheim	Munich	Palencia
Total skull length	109	—	—
Width anterior tip rostrum	34·7	—	—
Length rostrum to external nares	53·5	—	—
Width skull at external nares	79	—	69
Width rostral trough at external nares	49·8	—	32*
Length external nares to lambdoidal crest	29	33	34
Minimum width skull roof	48	40	45
Width at lambdoidal crest	98	—	—
Height lambdoidal crest to foramen magnum	47·3	—	—
Height lambdoidal crest to nuchal fossa	9·4	—	—
Height nuchal fossa	19·5	—	—
Width nuchal fossa	19	—	—
Width occipital condyles	30·5	—	—
Height foramen magnum	5·6	—	—
Width foramen magnum	14·1	—	—
Height lambdoidal crest to molar alveoli	50*	—	—
Width glenoid condyles	27	21	—
Length palatonarial border to rostrum tip	68	—	—
Width palate at P^3	15·8	7·7	—
Width palate at M^1	18·7	—	—
Width palate at M^3	15	10	—

Mandible

(Plates 4–5)

Material referred. 6404 : 13, incomplete horizontal rami with tusk fragments and cheek teeth; 6404 : 45, fragmented immature mandible with tusks and dentition; 6412 : 10, tuskless mandible with worn cheek teeth; B.M.(N.H.)M.26666, mandible with tusks and cheek teeth; 6419 : 16, symphysis fragment with tusk alveoli.

Description. Four nearly complete mandibles and a number of mandibular fragments have been collected from various sites at Gebel Zelten. None of the specimens is complete but sufficient information can be derived from the specimens to provide the following composite description.

The horizontal ramus is sigmoid, rising gently in front of M_3 and flexing ventrally at M_1 until at the tusk alveolus it subtends an angle of 115° to the alveolar border. The cheek teeth are erupted in almost parallel rows on the median dorsal surface of the horizontal ramus. The alveolar border is produced anteriorly to form a strong ridge extending from the third premolar to the tusk alveolus. These ridges converge anteriorly and enclose a gutter-like suprasymphysial depression similar to that of the elephantoids. The symphysis itself is broad and extends anteriorly from the vicinity of the posterior root of the third premolar. In one specimen (6412 : 10) a wide and shallow pit is preserved on the ventral and medial side of the horizontal ramus beneath the posterior root of P_3. The pit may represent the point of insertion of the anterior belly of the digastric muscle. On each ramus there are three mental foramina. In mandible 6404 : 13 the posterior foramen is slightly anterior to the front root of P^3; in 6412 : 10 it is level with the hind root of this tooth. In both specimens the anterior mental foramen is sited about 8 cms in front of the posterior mental foramen, and the intermediate foramen varies in location between the two.

Beneath the third premolar the horizontal ramus is oval in transverse section, being deeper than wide and slightly more convex laterally than medially. Beneath M_3 the horizontal ramus has flat and parallel lateral and medial sides and develops a small keel on the ventral surface. The dorsal surface of the horizontal ramus increases in width posteriorly and the lateral surface becomes the leading edge of the ascending ramus when level with M_3, from which it is separated by a wide, oval and concave platform.

The leading edge of the ascending ramus is nearly at right angles to the horizontal ramus. The coronoid process is small and directed anteriorly. The mandibular condyle is elevated only a short distance above the coronoid process and is a little wider than the latter is long. The condyle is almost cylindrical. The inferior and posterior borders of the ascending ramus are appreciably thicker than the adjoining bone. There is a pronounced notch beneath the dental foramen on the inferior border of mandible 6412 : 10 that may mark the insertion of the sternomandibular muscle. The medial surface of the ascending ramus is divided unequally by a ridge extending from the base of the mandibular condyle to the alveolar border beneath M_3. A second ridge descends posteriorly from the anteromedial face of the coronoid process and joins the first beneath the hind edge of the coronoid process. The triangular area thus enclosed serves for the insertion of the temporal muscle (which also occupies a depressed area of similar size on the lateral face of the ascending ramus). The masseter muscle inserts on the lateral surface of the angle of the jaw. The internal pterygoid muscle inserts similarly on the medial surface of the angle and the external pterygoid muscle inserts above the dental foramen and between the mandibular condyle and coronoid process. The digastric muscle inserts on the ventromedial surface of the mandible beneath and in front of the coronoid process.

COMPARISON WITH OTHER DEINOTHERE MANDIBLES. The degree of curvature and length of the mandibular symphysis varies appreciably with the various deinothere taxa. The mandibular symphysis of *Deinotherium giganteum* is longer and has a more vertically aligned symphysial region than that of *Prodeinotherium bavaricum*. *D. bozasi* of the African Quaternary has a relatively short mandibular symphysis but this is flexed at right angles and therefore more abruptly than in any other deinotheriid taxon. The symphysis of *D. levius* (here interpreted as synonymous with *D. giganteum*) is intermediate in length and degree of flexure between *D. giganteum* (*sensu stricto*) and *P. bavaricum* (Graf, 1957). Arambourg (1934) believed the apparently more acute flexure of *D. levius* separated this taxon from *D. giganteum*, and Laskarev (1944) deduced that *D. levius* had African rather than European affinities. The mandibular symphysis of *P. hobleyi* from Gebel Zelten is similar to that of *P. bavaricum*.

Sahni & Tripathi (1957) separated the two Asian deinotheriid taxa on the basis of the transverse section of the horizontal ramus level with M_3. In *D. indicum* the jaw bulges on either side of M_3, the lateral bulge being more pronounced and giving rise to a flat platform on the lateral side of this tooth and in front of the ascending ramus. In contrast, the jaw of *P. pentapotamiae* has a narrow and elliptical cross section. In this respect *P. hobleyi* from Gebel Zelten is similar to *D. indicum*.

Graf (1957) and Bergounioux & Crouzel (1962a) showed that the mental foramina of the mandible varied greatly in position. Those of *D. giganteum* and *D. bozasi* tended, however, to be sited more anteriorly than those of *P. bavaricum*. The mental foramina of the Gebel Zelten *Prodeinotherium* are also sited farther forward than in the examples of *P. bavaricum* quoted by Graf (1957 : 168).

TABLE 5

Prodeinotherium hobleyi mandible measurements

Left horizontal ramus (6412 : 10)	
Total length	63
Height at tusk alveolus	12·7
Height at P_3	13·3
Height at M_1	12·3
Height at M_3	11·1
Width at P_3	7·3
Width at M_1	7·7
Width at M_3	10·7

Left ascending ramus (6412 : 10)	
Length	22·6
Height at coronoid process	26
Height at mandibular condyle	29*
Mandibular condyle (6404 : 13)	
Length	4·7
Width	10·3

Dentition

(Text-fig. 7; Plates 4–5)

MATERIAL REFERRED. 6401 : 4, right maxilla with P^3–M^3; 6404 : 13, mandible with tusks and cheek teeth; 6404 : 44, immature skull with cheek teeth; 6404 : 45, fragmented immature mandible with tusks and cheek teeth; 6412 : 10, tuskless mandible with worn cheek teeth; M.26665, adult skull with cheek teeth; M.26666, mandible with tusks and cheek teeth; 6401 : 1, LM^3; 6404 : 14, LP^3–M^2 and RP^{3-4}; 6409 : 41, M^2 fragment; 6410 : 2, RP^4; 6412 : 39, LM^2; 6412 : 40, LM_1; 6412 : 54, LP^4; 6413 : 18, LM^3; 6416 : 120, tusk tip; 6416 : 130, tusk; 6421 : 2, LM^2; 6404 : 28, 6405 : 48, 6419 : 17, 6421 : 15, 6423 : 13, 6423 : 45, 6423 : 56, enamel fragments.

DESCRIPTION. Teeth are the most commonly preserved deinotheriid remains and differ sufficiently in size and morphology from other Cenozoic mammals to permit ready identification even on incomplete specimens. The terminology employed in previous descriptions of deinothere teeth has varied greatly from author to author. The teeth are basically lophodont, the lophs originating through coalescence of adjacent cusps in a bunodont ancestral stock. Terms used here are based on the standard cusp nomenclature (Osborn, 1907) and those used by Osborn for proboscidean teeth (Osborn, 1942). The terms are here used only to express topographic equivalence with the dental characters of other mammals and have no genetic significance.

Superior dentition. Downturning of the rostral region involved the posterior retreat of the external nares, accompanied by withdrawal of the premaxillae to line the floor of the rostral trough. The incisors, canines and anterior cheek teeth were lost during, if not before, the hindward migration of the premaxillae. All lophs and cingula on the upper teeth are rugose until worn. The lingual edges of the transverse lophs are taller than the labial edges and show more wear. A well developed facet is formed on the anterior surface of each transverse loph and extends for the entire width of the loph. Parallel facets are seen also on the anterior and posterior cingula when the tooth is worn sufficiently for these to occlude with the lower dentition.

The third premolar is equant and possesses two internal cusps and an ectoloph (text-fig. 7A). The protocone is the larger cusp and is separated from the hypocone by a deep but very narrow valley. The protocone extends labially and anteriorly to the base of the ectoloph, thus forming a low, incipient protoloph. The hypocone bears a small mesostyle on its anterolingual face. The hypocone is elongate labially but does not form a metaloph. The strong ectoloph is formed by the coalition of the paracone, metacone, and an intermediate cusp that is taller than either. The posterior end of the ectoloph is continuous lingually with the posterior cingulum that terminates lingually on the posterolingual face of the hypocone. The median valley is wide and open posteriorly; it is deepest between the labial bases of the protocone and hypocone. The anterior cingulum connects the base of the protocone to that of the ectoloph. There are no lingual or labia cingulla.

The fourth premolar is bilophodont and subequant, being longer than broad. The ectoloph is less strong than in the third premolar and the intermediate cusp is reduced to a swelling on the anterior face of the metacone. The transverse lophs are not straight, the protoloph being convex anteriorly and the metaloph convex posteriorly. Both lophs are connected labially with the ectoloph. From the posterior lingual face of the protocone a ridge extends posterolabially to the centre of the median valley and a similar ridge extends down the anterior face of the

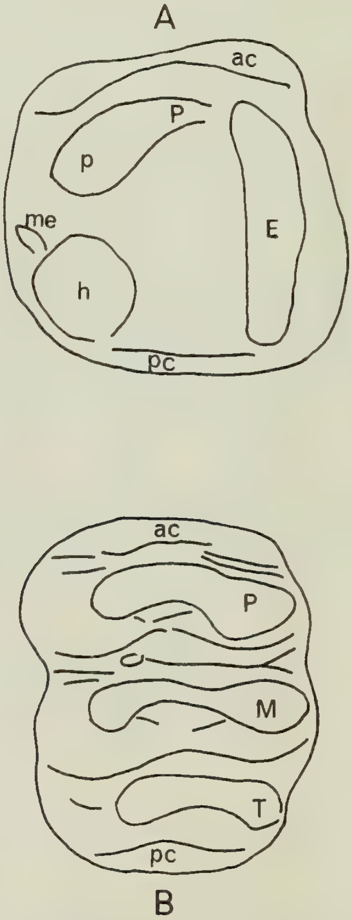

FIG. 7. *Prodeinotherium hobleyi* upper teeth. A = left P^3, B = right M^1; Not to scale.
ac = anterior cingulum, h = hypocone, me = mesostyle, p = protocone, T = tritoloph, E = ectoloph, M = metaloph, P = protoloph, pc = posterior cingulum.

hypocone. The metaloph of the fourth premolar is the only loph in the upper dentition to bear a posteriorly directed wear facet. The median valley is widest labially next to the ectoloph and narrows, opening lingually between the protoloph and metaloph. It is almost, but not quite, dammed by a small mesostyle on the anterior face of the hypocone. The anterior and posterior cingula are well developed. There is a minute internal cingulum.

The anterior molar is trilophodont and subrectangular, being longer than wide and narrowest posteriorly (text-fig. 7B). All three lophs bear ridges directed towards the midline of the tooth from their posterolingual and posterolabial edges. The tritoloph (posterior loph) is much less wide than either the protoloph or metaloph and the ridges from the posterolingual and posterolabial edges of the loph are less pronounced than in the protoloph or metaloph. Between the protoloph and metaloph the anterior median valley is blocked labially by a small bune between the paracone and metacone, and lingually by a short spur connecting the protocone to the hypocone. This spur bears a small mesostyle. The posterior median valley, between the metaloph and tritoloph, is much less deep. It is blocked lingually by a short spur connecting the lingual edges of the metaloph and tritoloph, and labially by the junction of sharp ridges extending down the posterior face of the metaloph and anterior face of the tritoloph. The anterior cingulum is strong but the posterior cingulum is less well developed than in the premolars.

The second molar is bilophodont and slightly longer than wide. The protoloph is similar to, but taller than, the metaloph. The centrally directed ridges on the hind face of the protoloph are well developed and stronger than in M^1. The ridge from the lingual edge of the loph extends beyond the midline of the tooth; that from the labial end of the loph is more posteriorly directed and fuses with a similar ridge extending from the crown of the metacone. The median valley is open labially but is bounded lingually by a short spur joining the protoloph to the metaloph. The postmetaloph ornamentation is rather complex. A strong ridge extends from behind the hypocone to join the lingual edge of the posterior cingulum. A more ventrally directed ridge connects that from the hypocone to a posterolabially directed ridge from the metacone, thus forming a subsidiary loph behind the metaloph. The posterior cingulum bears a large style on its labial extremity.

The third molar is subequant, and tapers posteriorly. Like the second molar it is bilophodont. The topography of the protoloph is similar to that of M^2. The metaloph is less wide than the protoloph, and the postmetaloph ornamentation is simpler. A ridge descends from the hypocone to the lingual termination of the posterior cingulum. The metacone gives off a strongly developed ridge that descends posteriorly and then centrally to the midline of the tooth to connect with the posterior cingulum. In some teeth the metacone ridge is also connected to the hypocone ridge and thus the postmetaloph ornamentation of M^3 is more variable than in M^2. There is no style on the posterior cingulum.

Inferior dentition. Tusks are present in mandibles 6404 : 13, M.26666, and 6404 : 45. The tusks are oval in transverse section with the long axis aligned anteroposteriorly. Enamel was preserved only on the tusks of the immature mandible (6404 : 45) where it covered the entire erupted surface of the tooth. The tusks in 6404 : 45 are short and nearly straight but in mandible M.26666 they curve downwards until the tip is nearly vertical. The dentine shows no 'engine turning' structure as in *Mastodon* but forms bands parallel to the periphery of the tooth.

As in the superior cheek teeth, all lophs, cingula and isolated cusps of the lower molars and premolars are rugose until worn. Except on P_4, all wear facets on the transverse lophids occur on the posterior surface. The labial edges of the lophids are less high but show more wear than the lingual edges.

The third premolar is triangular and tapers anteriorly. The protoconid is the largest and tallest cusp. It is elongate sagittally and is sited in the midline of the tooth. The protoconid is continued forwards as a high narrow ridge extending to the lingual edge of a very abbreviated anterior cingulum. It is also connected posterolingually to a tall metaconid. From the junction of the protoconid and metaconid, a narrow and less elevated ridge proceeds posteriorly to merge with an elongate hypoconid. This in turn connects with an elongate entoconid via a weakly developed, low, posterior cingulum. A C-shaped hypoconulid may or may not connect with the posterolabial edge of the entoconid. The protoconid and outer face of the ectolophid became worn more rapidly than the remainder of the tooth.

The fourth premolar is bilophodont and represents a wider and more elongate version of P_3. The protoconid and metaconid are set farther apart and are connected by a protolophid that is curved with the convex face posteriorly. The anterolingual extension of the protoconid extends more laterally than in P_3. The protoconid is also joined to the hypoconid by a low ectolophid. There is no hypoconulid but the hypoconid is connected to the entoconid by a hypolophid that is straighter and less tall than the protolophid. There are no well defined wear facets on the hypolophid but the lateral extremities become worn faster than the central portion and small wear facets occur on both sides of the lophid. The hypoconid is connected by a short spur to the strong posterior cingulum.

The first molar is trilophodont, the protolophid and hypolophid being wider than the tritolophid. A strong anterolingual ridge on the anterior face of the labial edge of the protolophid projects towards, but does not join, a weaker anterolabial ridge from the lingual extremity of the lophid. Similar but less strongly developed ridges may be traced on the anterior faces of the hypolophid and tritolophid. The anterior and posterior median valleys are open at both sides. The anterior cingulum is less well developed than the short, centrally placed posterior cingulum that stands proud at the rear of the tooth.

The second and third molars are bilophodont and are differentiated only by the posterior taper on the M_3 and the better developed posterior cingulum on that tooth. From the labial edge of the protolophid a strong medial ridge extends posteroventrally to meet the anterior cingulum. A similar but less strong ridge extends from the lingual extremity of the lophid. These ridges are duplicated in a less pronounced fashion on the anterior face of the hypolophid. The median valley is open at both ends. As in M_1, the wear facets on the lophids face posteriorly. The posterior cingulum of M_3 is less wide than that of M_2 but is taller, more curved, and extends farther posteriorly.

Table 6

Prodeinotherium hobleyi tooth measurements (in mm.)

Upper premolars

		6401: 4	6404: 14(l)	6404: 14(r)	6412: 55	M.26665(l)	M.26665(r)
P^3	ap	47·5	56·4	55·3+	—	46·5	43·7
	prot	—	55·0	—	51·1	—	—
	met	50·1	55·6	—	—	47·5	46·1
P^4	ap	—	47·1	—	—	47·9	44·9
	prot	—	62·7	64·0	—	58·5	58·4
	met	—	60·3	—	—	56·7	57·6

Upper molars

		6401: 1	6401: 4	6404: 14(l)	6413: 18	M.26665(l)	M.26665(r)
M^1	ap	—	68·6	76·6	—	70·5	71·5
	prot	—	58·8	60·7	—	62·5	62·9
	met	—	56·7	60·6	—	61·5	60·2
	trit	—	47·7	49·2	—	—	50·2
M^2	ap	—	67·8	73·2	—	70·6	73·1
	prot	—	67·9	69·0+	—	—	72·7
	met	—	66·5	64·0+	—	—	76·7
M^3	ap	75·7	67·2	—	59·3	72·8+	—
	prot	77·2	67·9	—	62·0	77·6	—
	met	66·9	62·6	—	—	73·9	—

Lower premolars

		6404: 13(l)	6404: 13(r)	6404: 45(l)	6404: 45(r)	6410: 2	6412: 10(l)	6412: 10(r)
P_3	ap	43·3	45·5	49·1	50·7	—	39·6	39·7
	tr	32·3	35·0	40·7	39·6	—	31·7	32·3
P_4	ap	54·4	53·1	—	58·9	—	44·3	44·7
	prot	43·0	43·9	—	46·9	38·4	38·6	39·4
	hyp	45·6	43·2	—	43·3	34·9	—	—

Lower molars

		6404: 13(l)	6404: 13(r)	6404: 45(l)	6404: 45(r)	6412: 10(l)	6412: 10(r)	6412: 39	6412: 40
M_1	ap	70·0	65·3	82·7*	—	55·0	55·3	—	55·1
	prot	48·8	47·0	47·4*	—	38·8	41·8	—	41·1
	hyp	51·0	49·1	48·2*	—	39·5	39·8	—	43·4
	trit	45·9	44·3	38·3	—	33·8	34·2	—	37·6
M_2	ap	—	71·9	—	76·3	57·0	54·8	—	—
	prot	65·5	61·6	—	61·1	50·3	50·4	52·8	—
	hyp	—	59·0	—	62·2	48·0	49·5	—	—
M_3	ap	—	—	—	84·0	66·9	67·8	—	—
	prot	—	—	—	63·4	54·1	54·9	—	—
	hyp	—	—	—	59·3	47·6	46·4	—	—

ap = greatest sagittal length:
prot = width at protoloph(id);
trit = width at tritoloph(id);
* = approximate measurement.
tr = transverse width;
met = width at metaloph(id);
hyp = width at hypolophid;

TOOTH FUNCTION IN DEINOTHERES. The function of deinothere tusks has yet to be satisfactorily explained. Conventional interpretations include pulling branches down to mouth level and digging for food. It is unlikely that deinothere tusks were used for digging for the following reasons. The tusks would fail to reach the ground unless the animal was either kneeling or standing at a lower elevation than the surface at which digging occurred. Such wear facets as have been observed are not consistent with a digging function. Food excavated from below ground surface would inevitably be contaminated with soil which would result in rapid attrition of the cheek teeth; no compensatory increase in hypsodonty of the deinothere cheek teeth has been observed.

The tusks of immature deinotheres are covered by enamel. Enamel production apparently ceases shortly after the eruption of the tusks. The absence of enamel on the tusks of mature deinotheres suggests that the enamel-bearing portion was subsequently removed by wear. I have observed wear facets in two places on deinothere tusks—on the posterior surface of the tusk tip (*P. hobleyi*) and on the anteromedial surface of the tusk tip (*P. hobleyi, P. bavaricum, D. bozasi*). The anteromedial facets may be attributed to constant abrasion by the proboscis but might conceivably have been produced during the action of stripping bark or branches from vegetation.

A detailed description of the cheek tooth function in deinotheres is in the process of preparation. A summary of the preliminary conclusions is given below. Deinothere cheek teeth occlude orthally and may be functionally divided into anterior crushing teeth and posterior shearing teeth. In the premolars some shearing is effected during occlusion of the ectoloph and ectolophid. The transverse crests on the premolars serve to prevent anterior dislocation of the jaw during the occlusal stroke of the mandible and perform a crushing function during the recovery stroke. The transverse crests of the deciduous fourth premolars and of the molars have well developed shearing facets—on the anterior surface of the lophs and rear of the lophids. These facets are maintained until the transverse crests have been almost completely removed by wear. In unworn teeth the facets are aligned almost vertically but become progressively more horizontal with wear. The change in angle of the shear facet is seen not only between individuals of different maturity but also within single tooth rows, the facets on the posterior end of the tooth row being oriented more vertically than on the anterior molars.

The anterior crushing battery and posterior shearing battery are reconstituted three times during the life of the individual as follows:

	anterior battery	posterior battery
Juvenile animal	DP2–3	DP4
Immature adult	P3–4	M1
Mature adult	P3–4, M1	M2–3

The anterior trilophodont molar performs different functions at different stages of wear. Initially it serves as a shearing tooth in contrast to the crushing premolars. By the time the second and third molars are fully functioning the anterior molar is often too worn to provide an efficient shearing action and becomes incorporated into the anterior crushing battery.

The width of the anterior molar, its attitude in the alveolus, and its alignment in the tooth row all suggest that it functions primarily as a posterior premolar rather than as an anterior molar. The shearing action of this tooth is of limited duration but sufficient to cope during the transition between deciduous and permanent dentition. The bifunctional nature of the tooth row may well explain why deinotheres failed to develop horizontal tooth replacement as in the elephantoids.

Axial skeleton

(Text-figs 8–13)

Material referred. M.26667h, left rib head; M.26667i, right neuropophysis of third cervical vertebra; 6419 : 15, atlas vertebra; 6424 : 79, axis vertebra.

Description. *Atlas vertebra.* The atlas vertebra of *Prodeinotherium hobleyi* (text-fig. 8, 6419 : 15) is smaller than that of *Mastodon angustidens* (6412 : 185) from Gebel Zelten. Although the transverse processes of the mastodont atlas are incomplete the *Prodeinotherium* atlas was probably wider. The facets for articulation with the occipital condyles are comma-shaped in both specimens but the mastodont facets are larger, relatively taller, less wide and apparently more concave. Differences on the dorsal edge of the neural arch are especially pronounced. The neural spine of the mastodont atlas forms an elongate transverse ridge with large and widely separated scars for the insertion of the rectus muscles. The *Prodeinotherium* atlas spine is a shorter, blunt protruberance that is bounded by rectus muscle scars that are smaller and face more ventrally than in *Mastodon*. The transverse processes of the mastodont specimens are incomplete but were apparently more horizontal than those of *Prodeinotherium* and are sited higher on the neuropophysis, extending for some 4 cms above the dorsal edge of the axis facet. The odontoid fossa of the mastodont atlas is also incomplete but appears to rise more steeply anteriorly and to be more concave than that of *Prodeinotherium*.

The atlas attributed to *Prodeinotherium* does not articulate well with a *Prodeinotherium* axis vertebra (6424 : 79) from an unknown locality at Gebel Zelten, mainly due to differences in the articular facets. The general proportions of the occluding facets and odontoid fossa and processes are however sufficiently similar for the poor articulation to be attributed to variation between individual specimens.

Table 7

Atlas vertebra measurements

Parameter	*Prodeinotherium hobleyi* 6418:15	*Mastodon angustidens* M.26656	*Loxodonta africana* 1961.8.9.82
Maximum length	10·4	10.7+*	7·8
Maximum height	17·2	20·0	17·9
Width at transverse process	28·7	24·3+	30·4
Width at occipital facets	18·4	20·7	21·3
Width neural canal	6·1	7·3	8·0
Height neural canal	5·0	5·3	3·9
Width odontoid fossa	5·6	6·5	7·3
Height odontoid fossa	6·2	5·6	6·2
Width at atlas facets	16·7	16·3*	17·7

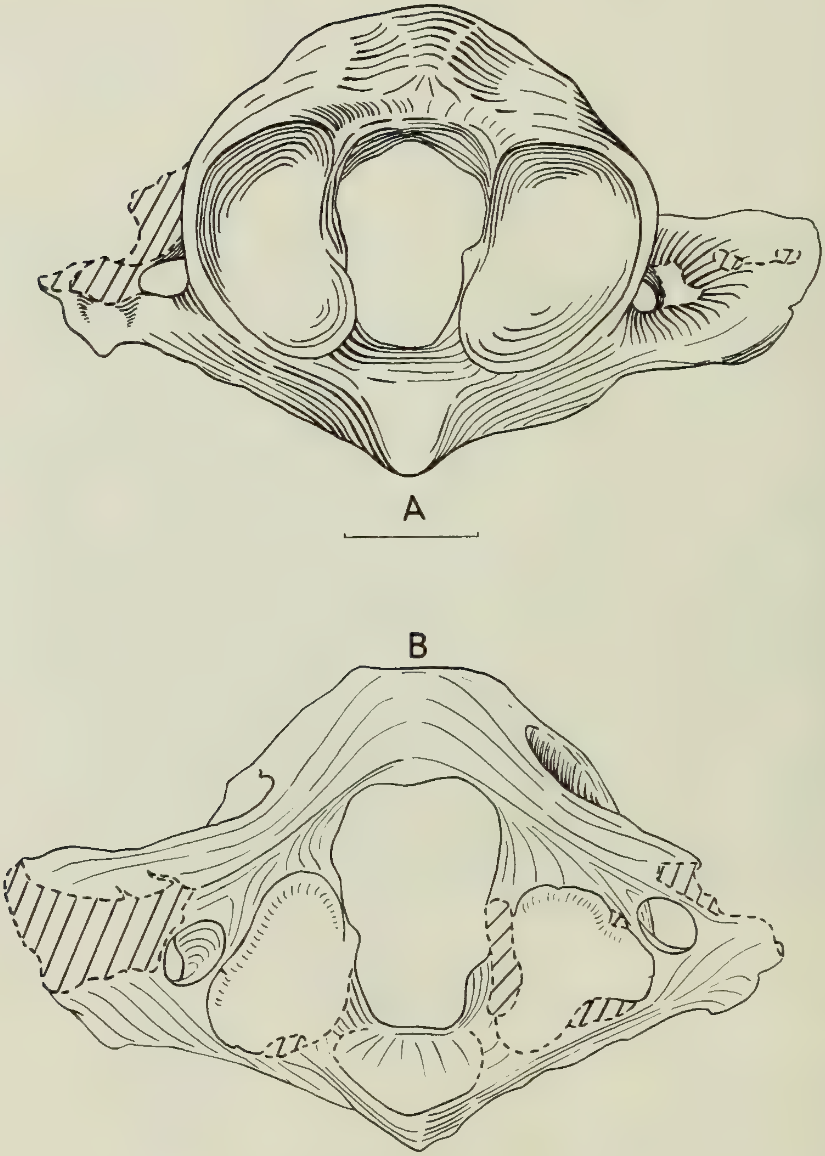

FIG. 8. *Prodeinotherium hobleyi* atlas vertebra.
A = anterior view, B = posterior view. Scale = 5 cm.

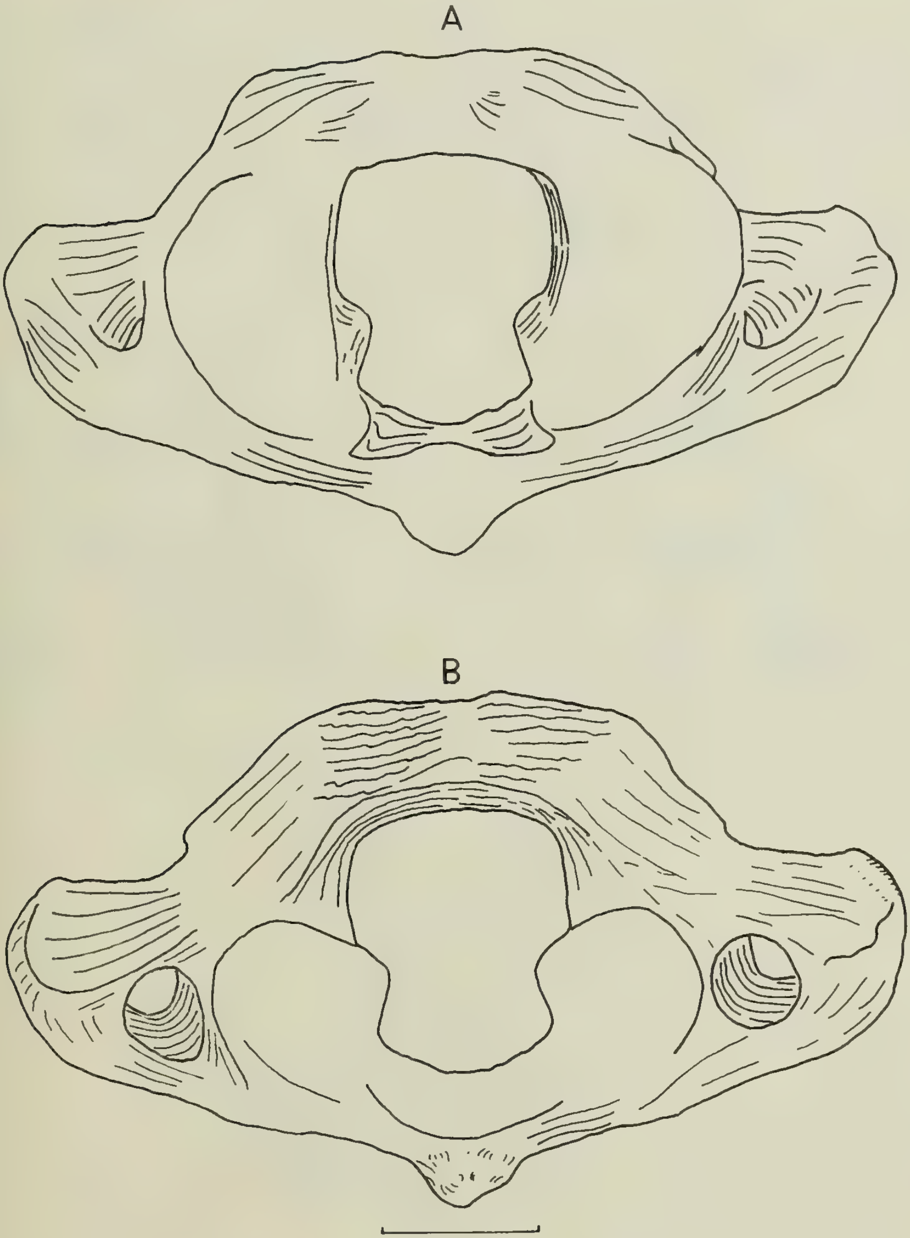

FIG. 9. *Loxodonta africana* atlas vertebra.
A = anterior view, B = posterior view. Scale = 5 cm.

Axis vertebra. The sole deinotheriid axis from Gebel Zelten (6424 : 79) is incomplete dorsally and ventrally (text-fig. 10). In overall size it is slightly smaller than the axis vertebra of the extant African elephant (text-fig. 11) but the odontoid process, although eroded, is longer and stouter in *Prodeinotherium*. The transverse processes are broken at their bases and the entire ventral half of the centrum is missing. The cephalic articular surfaces are oval, extending posteroventrally from above the odontoid process. It is not clear whether, as in *Loxodonta*, the articular facets extend to meet below the odontoid process because they are incomplete. The neural canal is circular in transverse section. The neural arch is notched anteriorly and posteriorly for the passage of the second and third cervical spinal nerves, the posterior notch being the deeper.

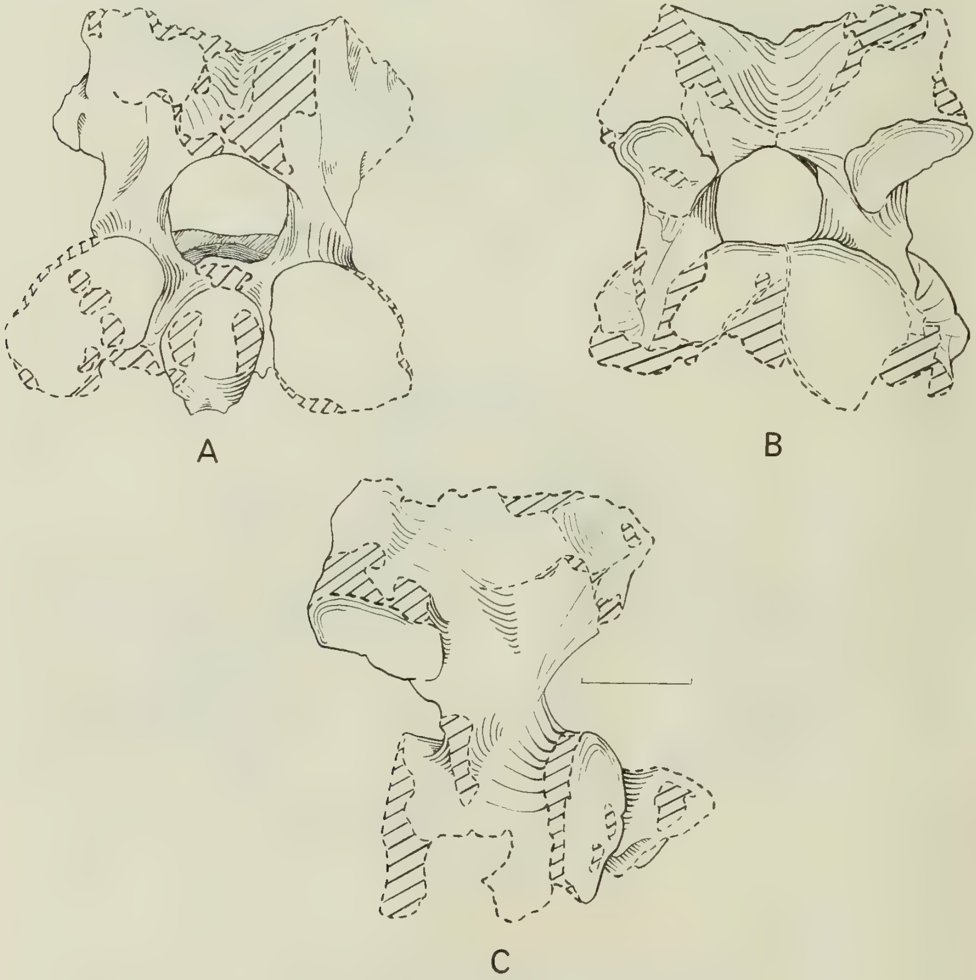

Fig. 10. *Prodeinotherium hobleyi* axis vertebra.
A = anterior view, B = posterior view, C = right lateral view. Scale = 5 cm.

The spine is the most diagnostic feature of the *Prodeinotherium* axis. In the extant elephants 'the neuropophyses blend together above and develop a thick bifurcate spine before coalescing with the centrum' (Owen, 1866 : 547). In the Gebel Zelten axis the neuropophyses are less tall but longer anteroposteriorly than in *Loxodonta*. The bifurcation of the spine is extreme, beginning at the anterior tip of the spine and diverging at an angle of 55° (cf. 30° in *Loxodonta*). The twin crests

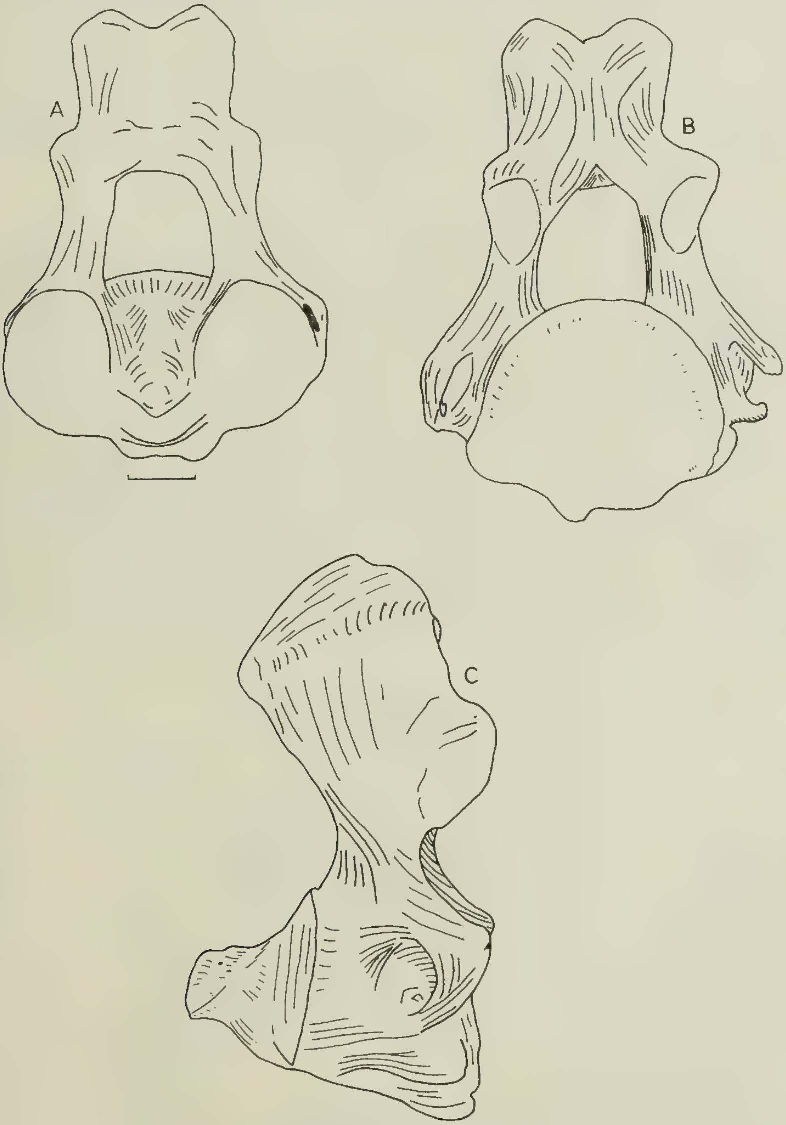

FIG. 11. *Loxodonta africana* axis vertebra.
A = anterior view, B = posterior view, C = left lateral view. Scale = 5 cm.

thus formed ascend backwards less steeply than in the elephant but reach farther posteriorly and are separated by a U-shaped valley that widens posteriorly and descends at an angle of nearly 30° from the horizontal. In *Loxodonta* this valley appears only at the posterior portion of the spine and is horizontal. The postzygapophyses of the elephant axis are convex; the greater part of the articular surface faces ventrolaterally but the dorsomedial corner faces posteriorly. Much of the articular surfaces of the zygopophyses of the Gebel Zelten *Prodeinotherium* axis are eroded but they are seen to be larger than in the elephant, to be concave and to face ventrolaterally. A small triangular facet may be discerned along the dorsomedial edge of, and at right angles to, the main articular surface but this may have served for the attachment of muscles or ligament rather than for articulation. Above the postzygapophyses much of the bone is missing but this region of the spine must originally have been greatly swollen.

Although the neuropophyses are appreciably wider and longer than those of the elephant, the centrum is only slightly longer. It is not until the relative areas of the neural canals are taken into consideration that the axis of *Prodeinotherium* is seen to be more massive and appreciably longer than that of the African elephant. The larger surface of the neural spine affords a greater area of attachment for the *rectus capitus posterior major* muscle, *obliquus capitus inferior* muscle, *semispinalis capitus* and *semispinalis cervicus* muscles. All four muscles serve to extend the head on the neck or, acting unilaterally, to rotate or flex the head on the neck. The narrow width of each diverging supraspinous crest suggests that the nuchal ligament was inserted only on the posterior portion of the dorsal surface of the supraspinous crest. The great width of the spine reflects the great width of the nuchal ligament that is in turn reflected by the wider fossae for the nuchal ligament on the occiput of *Prodeinotherium* than in elephantoids. The relatively low dorsoventral height of the spine may reflect the elevated condition of the occipital condyles and/or the less elevated head of deinotheres.

TABLE 8

Axis vertebra measurements

Parameter	*Prodeinotherium hobleyi* 6424:79	*Loxodonta africana* 1961.8.9.82
Maximum length	17·1	13·4
Maximum width	17·5+	17·5
Maximum height	17·7+	24·6
Width at atlas facets	17·6+	17·2
Width neural canal	5·2	6·2
Height neural canal	5·0	5·8
Width odontoid process	3·9+	3·4
Height odontoid process	4·7	3·6
Maximum length neuropophysis	15·2	11·9
Minimum length neuropophysis	5·5	3·6
Minimum width neuropophysis	15·3	11·7
Height neuropophysis above neural canal	7·6+	8·1
Length postzygopophysis	5·2+	5·5
Width postzygopophysis	5·2+	3·7

Third cervical vertebra. An incomplete right neuropophysis of a third cervical vertebra M.26667i was associated with immature *Prodeinotherium* skeletal elements from Gebel Zelten site D. The specimen (text-fig. 12) is not well preserved but incorporates the region between the neural spine and the vertebrarterial canal. The neural spine is very low and could have been elevated only slightly above the valley separating the two wings of the axis spine. The neural canal is compressed dorsoventrally. The neural arch is longer anteroposteriorly but less stout than in *Loxodonta.* The prezygapophysis is convex and faces anterolaterally. The postzygapophysis is concave and faces ventrally. Both zygapophyses are aligned more horizontally than in *Loxodonta.* The neural arch is notched anteriorly and posteriorly for the passage of the spinal nerves, the posterior notch being deeper and extending

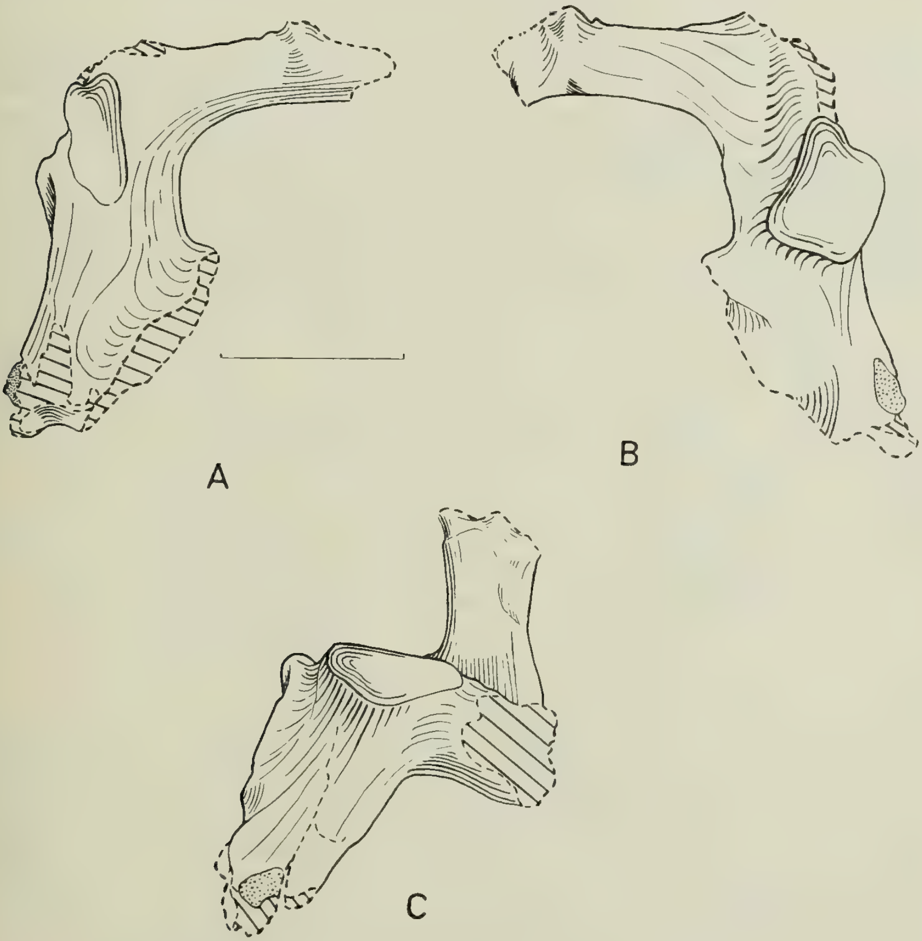

FIG. 12. *Prodeinotherium hobleyi* third cervical vertebra.
A = anterior view, B = posterior view, C = lateral view. Scale = 5 cm.

to the dorsal edge of the vertebrarterial canal. The surface of the bone is not well preserved and muscle attachment areas cannot be detected.

It is interesting that the articular surfaces of the zygapophyses have reversed curvature when compared to the elephantoids in which the postzygapophysis and not the prezygapophysis is convex. This is believed to have some bearing on the direction of movement of the neck in elephantoids as opposed to deinotheres. The centra of the cervical vertebrae of the Gebel Zelten deinothere shows some flattening anteroposteriorly as in the elephantoids but the neuropophyses are considerably more massive. Taking into consideration the diameter of the neural canal, the cervical vertebrae of the Gebel Zelten *Prodeinotherium* were more elongate than those of *Loxodonta*.

TABLE 9

Measurements of *third cervical vertebra*

Parameter	*Prodeinotherium hobleyi* M.26667i	*Loxodonta africana* 1961.8.9.82
Maximum length neuropophysis	7·7+	7·1
Length neuropophysis at neural arch	3·1	2·8
Width transverse process above vertebrarterial canal	2·8	1·9
Width neural canal	7·0+	6·8
Height neural canal	4·4	5·7
Height neural arch above centrum	5·9	9·0

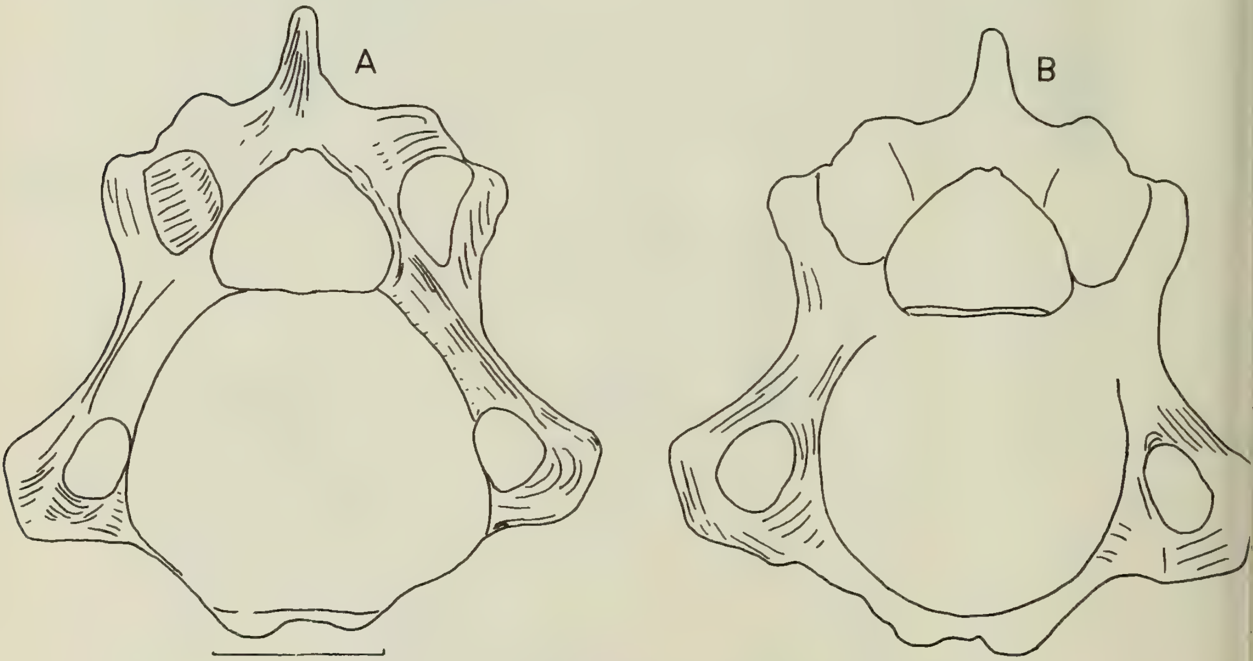

FIG. 13. *Loxodonta africana* third cervical vertebra.
A = anterior view, B = posterior view. Scale = 5 cm.

Rib One left rib was collected with the immature *Prodeinotherium* skeleton from site D. Other rib fragments were noted but were too incomplete to warrant collection. The head of the rib M.26667h is large, rounded and divided by a deep transverse groove into two convex oval facets for articulation with two thoracic vertebrae. The transverse groove is widest medially, and the cranial articulation facet is larger than the caudal. The neck is short and a little wider than the head. On the dorsal edge of the neck is an oval, slightly convex tubercule that articulates above the caudal facet of the head. On the caudolateral side of the tubercule is a rounded prominence, one fourth the size of the tubercle, that may have served for attachment of the longissimus dorsi muscle. The shaft of the rib extends ventrolaterally from the neck but flexes downwards at nearly 40° at the angle. The dorsal surface of the angle bears an elongate prominence for the attachment of the iliocostal muscle. On the cranial surface of the rib, between the head and the angle, there are two elongate fossae. On the caudal surface a deep groove appears midway between the head and angle near the lateral border of the shaft. A transverse section of the shaft proximal to the angle resembles the shape of an hourglass; distal to the angle it is concavoconvex (concave caudally). Distal to the caudal depression the cranial face turns laterally and the transverse section becomes oval and progressively flattened towards the end of the rib. Extending over the cranial surface of the shaft from the angle are a number of irregular prominences that serve for the attachment of various parts of the serratus posticus muscles.

The bicipital head of the rib suggests that it was articulated towards the front of the rib cage.

TABLE 10

Measurement of *Prodeinotherium rib* M.26667h

Parameter	*Dimension*
Length head	5·3
Width head	5·0
Width neck	5·2
Length neck	3·7
Length neck to angle	10·7
Length at angle	6·8
Breadth at angle	2·7

DISCUSSION. In mammals generally, only one muscle is attached to the anterior face of the arch of the atlas vertebra. This muscle, variously recorded as the *rectus capitis dorsalis minor* (Sisson & Grossman, 1947), *rectus posterior minor* (Jayne, 1898), and *rectus capitis lateralis posterior minor* (Shindo & Mori, 1957) inserts on the occiput lateral to the nuchal fossa and serves to extend the head on the neck. The reduced width of the neural spine of the deinothere atlas compared to that of elephantoids is due, at least partly, to the fact that the sites of origin of the rectus muscles are closer together and face upwards and outwards rather than forwards. The line of action of the muscles is thus less horizontal and more vertically aligned than in *Mastodon* or the elephants. The change in line of action of the musculature reflects the different geometry of the occiput of *Prodeinotherium* which has a more dorsally placed nuchal fossa than has that of the elephantoids. The more posteriorly inclined transverse processes may be partly due to a more vertical alignment of the muscles extending from the transverse process to the occiput, or may reflect the importance of muscles originating from the ventral surface of the transverse process to insert on the basicranium and paroccipital process.

The Gebel Zelten *Prodeinotherium* axis differs in many features from that of the elephantoids, the more striking differences being associated with the development of the neuropophyses. The muscles attaching thereto serve to move both the neck on the thorax and the head on the neck. The cross sectional area of the anterior opening of the neural canal of the axis vertebra of *Loxodonta* (ca. 4000 mm^2) is half as large again as that of the Gebel Zelten deinothere axis (ca. 2600 mm^2) and if this area may be taken to suggest the relative size of these two mammals (cf. Radinsky, 1967) then the Gebel Zelten deinothere, although smaller than the African elephant, has much larger and longer neuropophyses than the living animal. It is obvious therefore that the axis of *Prodeinotherium* plays a more important role in the move, ment of the head and neck than that of *Loxodonta*.

Five major muscles are attached to the axis spine. The *rectus capitis posterior major*, *obliquus capitis inferior*, and *semispinalis capitalis* originate on the axis and move the head about the atlantooccipital joint; the *scalenus* and *semispinalis cervicus* insert on the axis and move the head on the thorax. The lamellar portion of the nuchal ligament also inserts on the spine of the axis. Three muscles possess considerably larger attachment areas on the spine of the *Prodeinotherium* axis than on that of the elephant. These are the *obliquus capitis inferior*, the *rectus capitis posterior minor* and the *semispinalis cervicus*. The former rotates, extends and fixes the atlantooccipital joint (and thereby the head), while the *rectus capitis* extends the head and the *semispinalis cervicus* extends the neck. All three are attached to the upper part of the neuropophysis. That the spine is less elevated than in *Loxodonta* suggests that its function as a lever for moving the head on the thorax is less important than its capacity to move the head on the neck. The external walls of the spine are orientated more laterally than in *Loxodonta* thus affording a more nearly perpendicular line of action for the muscles moving the head and thereby enhancing the mechanical efficiency of these muscles. The sagittal length and divergent nature of the neural spine of the axis also affords a greater area of attachment for the digitation of the lamellar portion of the nuchal ligament.

The postzygapophyses of the axis and zygapophyses of the succeeding cervical vertebrae of deinotheres are more horizontally aligned than in the elephantoids. The curvature differs also—the postzygapophyses of deinotheres are concave and the prezygapophyses convex in direct contrast to the condition normally found in the elephantoids. Thus while the zygapophyses of the anterior cervical vertebrae of elephantoids permit an upward flexure of the neck, those of *Deinotherium* and *Prodeinotherium* flex in the opposite direction. The differences in direction of flexure may be related to the different ways in which the tusks function in deinotheres and elephantoids.

The centrum of the axis is slightly longer in *Prodeinotherium* than in *Loxodonta* and is appreciably longer when the area of the neural canal is used as a basis for comparison. The neural arch of the third cervical vertebra from Gebel Zelten is also longer than its equivalent in *Loxodonta* and it is probable also that this was true of the remaining vertebrae of the neck. Increase in the length of the neck amounts to a decrease in the lever arm of the musculature supporting the head on the neck and moving the head on the thorax. The decrease in lever arm of these muscles reduces their mechanical efficiency, and a larger and stronger musculature is therefore required to support the head on the neck. This is reflected by the large area of insertion of the *semispinalis cervicus* muscles in *Prodeinotherium*. Without access to the cervical vertebrae of *Deinotherium* one cannot deduce whether the relatively long neck of the Gebel Zelten deinotheres is a primitive feature, the neck becoming shorter and mechanically more efficient in later forms, or whether it was a functional adaptation to permit the head to be nearer the ground and thereby enhancing the potential use of the tusks for feeding.

The thoracic vertebrae of *Deinotherium* are incompletely known, the anterior thoracics being best known from the skeleton of *D. 'gigantissimum'* (= *D. giganteum*) from the Pliocene of Manzati, Rumania. The neural spines of these vertebrae are inclined steeply posteriorly. Slijper (1946) pointed out that the neural spines act as levers to transmit muscular force to the centra. The force applied determines the height and direction of the spines. Increase in total body size is accompanied by a relative increase in muscle strength, the size and shape of the spines being therefore dependent also on body size, weight of the head, and length of the neck. The most favourable direction of the neural spine is perpendicular to the muscular force acting on the spine, but intermediate directions are achieved when two or more forces act in different directions upon one spine. In the elephant three main forces are applied to the neural spine of the anterior thoracic vertebrae by the nuchal ligament, the *spinalis dorsi*, and the *multifidus spinae* muscles. Tension in the nuchal ligament exerts a force pulling the spines anteriorly whilst contraction of the muscles pulls the spines posteroventrally.

The funicular portion of the nuchal ligament exerts most of its force on the anterior thoracic vertebrae. The anterior thoracic neural spines of *Loxodonta* are more perpendicular to the centra than those of *Elephas*, although in both animals the spines slope backwards. This indicates that the nuchal ligament of *Loxodonta* is more horizontally aligned and, conversely, that the head of *Elephas* is more elevated with regard to the anterior thoracic vertebrae. Because the nuchal ligament functions most effectively when the lever arm (neural spine) is perpendicular to the line of action of the ligament one may deduce that mammals whose heads are sited above the withers will have backward pointing spines whereas those mammals whose skulls are on the same horizontal plane as the withers will have upright spines. The few mammals with skulls held below the level of the withers will also have vertical neural spines but because the line of action of the ligament will not be perpendicular to the spines the lever arm of the ligament must increase to compensate for reduction in efficiency. The neural spines of these mammals will therefore be correspondingly longer than those of mammals in which the skull and shoulders are level.

The vertebral column of *D.* '*gigantissimum*' was restored and mounted by de Pauw (Stefanescu, 1907; Pl. 1). The neural spines of thoracic vertebrae 2–5 are far more steeply inclined than in those of either of the extant elephants. The original specimens from Manzati, Rumania, were incomplete and their exact length cannot be determined. Backward inclination of these neural spines may be interpreted in two ways: either the head of the deinothere was carried above the shoulders (the backward inclination being influenced by the line of action of the nuchal ligament) or the vertebral column was rigid (the position of the spines being determined by the multifidus muscles). Total length as well as the angle of inclination of the neural spines must be considered before either alternative can be fully investigated. With regard to the rigidity of the vertebral column, none of the extant graviportal mammals can flex their lumbar and thoracic vertebrae. In view of the large size of the deinotheres it seems likely that the vertebral column would have been similarly modified and perhaps the extreme spinal inclination suggests extreme inflexibility.

Appendicular skeleton

(Text-figs 14–16)

MATERIAL REFERRED. M.26667a, distal end of fibula; M.26667b, right ulna; M.26667c, proximal end of right humerus; M.26667d, right femur; M.26667e, left ulna; M.26667f, scapula; M.26667g, left innominate; M.26667j, proximal and distal end of left radius; M.26667k, distal end of right humerus; M.26667l, distal end of left humerus; 6405 : 98, left cuneiform.

DESCRIPTION. *Scapula.* An almost complete right scapula (M.26667f, text-fig. 14) was associated with the immature skull from Gebel Zelten site D. The left scapula was also present but was partly overlain by skull 6404 : 44 and was destroyed during excavation of the latter. The fragility of scapula M.26667f resulted in the collapse of the vertebral border and cranial and caudal angles during transportation from the site but these portions were subsequently restored with the aid of photographs taken at the site.

The articular fossa is broad and concave. The scapular tuberosity is poorly developed but the coronoid process is well defined. The scapular notch is deeply indented. The spine divides the lateral surface of the scapula into supraspinous and infraspinous fossae of similar proportions to those of *Elephas maximus.* The spine attains its highest elevation in its ventral third at the point of divergence of the acromion and metacromion. From here it descends gradually to the neck and caudal angle. Near the neck the cranial surface of the spine is concave but becomes convex near the cranial angle. The reverse is true of the caudal surface.

Although the scapula is similar in size to that of the Indian elephant, the caudal angle is sited dorsal to the point of divergence of the acromion and metacromion. In the Indian elephant the base of the acromion is level with the caudal angle. The

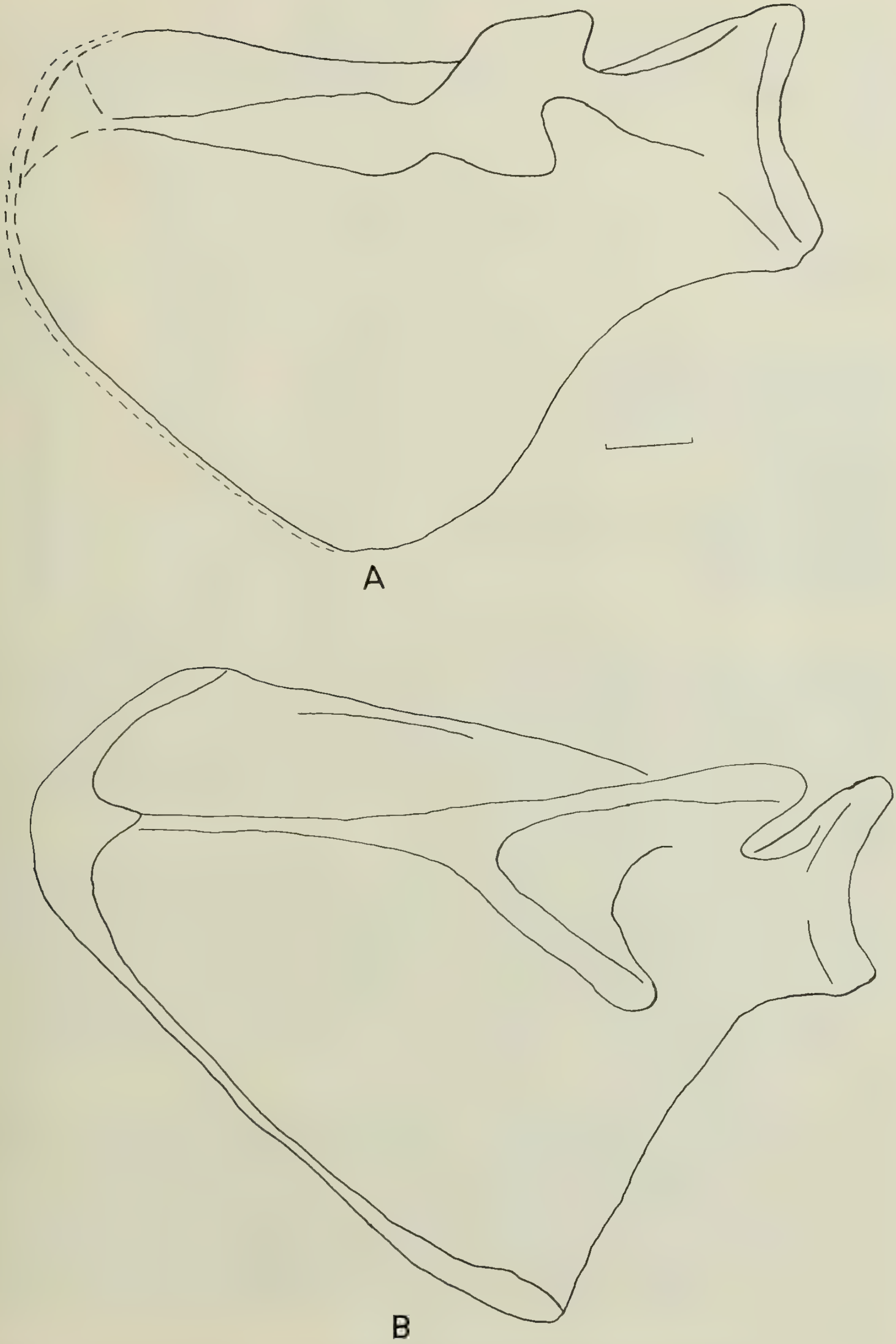

FIG. 14. Right scapula of (A) *Prodeinotherium hobleyi* and (B) *Elephas maximus*. Scale = 5 cm.

head of the *Prodeinotherium* scapula is wider and less concave than that of the elephant and the spine ascends more gently from the neck than in *Elephas*. The scapular notch is deeper and the scapular tuberosity less pronounced than in *Elephas*.

TABLE 11

Scapula measurements

Parameter	*Prodeinotherium hobleyi* M.26667j	*Elephas maximus* U.B.20189
Length head to vertebral angle	52+	62
Transverse width at caudal angle	35	42
Length caudal angle above head	25	15
Length caudal angle behind spine	26	30
Length spine	40	44
Length acromion	9	17
Length metacromion	6	16
Maximum width spine behind metacromion	5	3·7
Width head (straight)	15·3	14·3
Width head (curved)	17	16
Depth head	10*	8·3

Humerus. The distal extremities of a right and left humerus M.26667k and M.26667l) were associated with the immature skull 6404 : 44. They are complete from the condyles to the deltoid tuberosity and proximal end of the lateral supracondyle ridge. This part of the bone is slightly shorter proximodistally than the equivalent part of the humerus of the Indian elephant but is appreciably wider and deeper suggesting a larger area of origin of the many flexor and extensor muscles that arise from this portion of the humerus.

In cranial aspect the distal end of the musculospiral groove is seen to curve laterally towards the proximal end of the lateral supracondylar ridge. This is a strong ridge, straighter and more salient laterally than its equivalent in the elephant. As in *Elephas* the lateral epicondyle does not project very far laterally but it is stronger cranially in *Prodeinotherium*. Medial to the lateral epicondyle there is a small but deep fossa separated by a low ridge from the very wide but shallow coronoid fossa. The median epicondyle of the trochlea is larger than the lateral, the disparity in size being more pronounced than in *Elephas*.

In caudal aspect the lateral and medial epicondyloid ridges are considerably wider than their counterparts in *Elephas*, as are also the epicondyles. Thus, despite the great overall width of the distal portion of this bone, the olecranon fossa is considerably narrower than in *Elephas*. In *Elephas* the epiphysial suture between the median epicondyle and the condyle is aligned diagonally whereas in *Prodeinotherium* it runs medially, thereby increasing the area of the condyle. The anconeal process of the *Prodeinotherium* humerus is narrower but no more salient than that of *Elephas*.

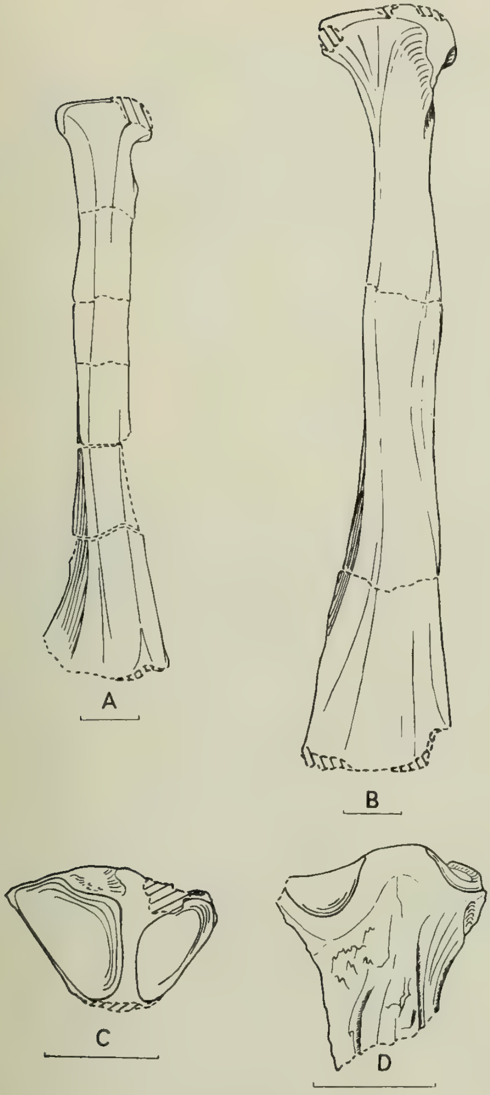

FIG. 15

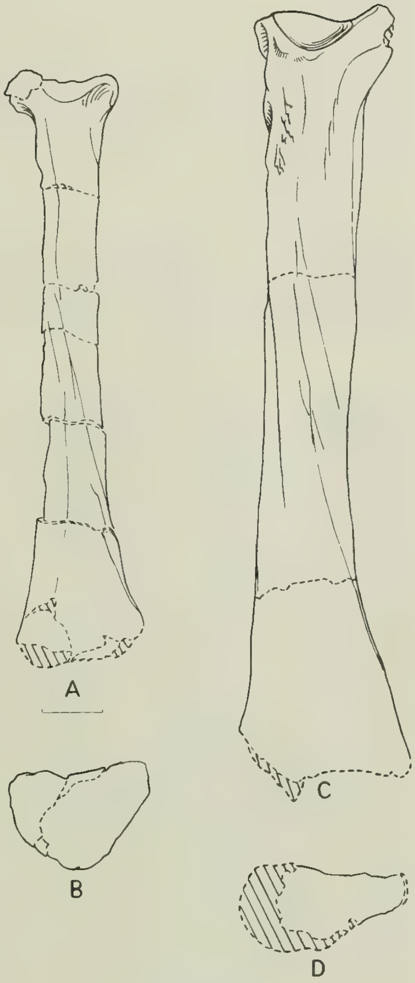

FIG. 16

FIG. 15. Radius of *Prodeinotherium hobleyi* and *Mastodon angustidens*.
A = *P. hobleyi* left radius (M.15429), cranial view
B = *M. angustidens* right radius (6412 : 166), cranial view
C = *P. hobleyi* head of left radius (6404 : 41), dorsal view
D = *P. hobleyi* head of left radius (6404 : 41), caudal view

FIG. 16. Radius of *Prodeinotherium hobleyi* and *Mastodon angustidens*.
A = *P. hobleyi* left radius (M.15429), caudal view
B = *P. hobleyi* left radius (M.15429), distal view
C = *M. angustidens* right radius (6412 : 166), caudal view
D = *M. angustidens* right radius (6412 : 166), distal view
Scale = 5 cm.

TABLE 12

Humerus measurements

Parameter	*Prodeinotherium hobleyi* M.26667k	*Prodeinotherium hobleyi* M.26667l	*Elephas maximus* U.B.20189
Width at dorsal edge of lateral epicondyle	18·5	18·3	14·6
Length from lateral epicondyle to distal end of condyle	19·7	19·7	14·6
Width at median epicondyle	20·5	20·9	19·0
Length from median epicondyle to distal end of median condyle	14·0	13·4	10·5
Width of articular surfaces on condyles	16·2	16·7	15·3
Depth at median epicondyle	14·2	14·8	13·4
Minimum width shaft above lateral epicondyle	9·4	10·1	7·7
Minimum depth shaft above lateral epicondyle	9·2	9·3	7·6
Depth of articular surface of median condyle	12·0	10·2	12·1
Depth of articular surface of lateral condyle	10·2	10·2	11·0

Radius. Only two proboscidean radii have been collected from Gebel Zelten—the head and neck of a left radius of *P. hobleyi* (text-fig. 15C and D; M.26667j) and a nearly complete right radius (M.26654; text-figs 15 and 16) of *Mastodon angustidens*. Two left proboscidean radii from East African Miocene localities are present in the collections of the British Museum (Natural History). That from Rusinga (B.M.(N.H.)M.21872) was attributed to *P. hobleyi* by MacInnes (1942) but belongs to *Mastodon angustidens*. The other specimen (B.M.(N.H.)M.15429) is from Maboko Island and belongs to *Prodeinotherium* (text-figs 15 and 16).

The proximal articular surface of the radius of *Mastodon angustidens* is trapezoidal in outline, with the medial side longer than the lateral. The capitular depression for articulation with the humerus is not large and extends through the centre of the articular surface parallel with the caudal and cranial edges. At right angles and distal to the capitular depression, articulation facets for the ulna occur on the medial and caudal sides, the medial facet being the smaller. Beneath the neck and caudal edge of the median articulation facet for the ulna, the radius is swollen to produce a radial tuberosity for the insertion of the *biceps brachii* muscle. This tuberosity is more pronounced than in *Prodeinotherium* or *Elephas*. Immediately below the radial tuberosity the shaft is approximately rectangular in transverse section, the caudal and cranial edges being the longest and the lateral edge being slightly shorter than the medial. Distally the medial and lateral edges diverge and the shaft is compressed craniocaudally but whereas the shaft of *M. angustidens* retains this shape throughout its length, that of *Prodeinotherium* becomes more equant in its distal half.

Halfway down the shaft of *M. angustidens* the medial edge of the cranial surface is flattened for the insertion of the pronator teres muscle. The interosseous crest extends down the medial side of the caudal face from beneath the radial tuberosity. Distal to the insertion of the *pronator teres*, and at the proximal end of the distal third of the shaft, the interosseous crest diverges, a strong ridge extending towards the medial edge of the epiphysis and a weaker ridge towards the lateral. Lateral to the interosseous crest is a deep depression extending from the radial tuberosity to the distal fourth of the bone.

The radius of *Prodeinotherium* is smaller than that of *M. angustidens* and is less straight proximodistally and craniocaudally. The radial tuberosity is comparatively less well developed and the interosseous ridge diverges halfway down the shaft. The distal extremity is less wide and deeper craniocaudally than in *M. angustidens.* The radii of both *M. angustidens* and *P. hobleyi* are of similar length to the radius of *Elephas maximus* but the shafts are much wider and the entire bone stouter.

TABLE 13

Radius measurements

Parameter	*Prodeinotherium hobleyi*		*Mastodon angustidens*		*Elephas maximus*
	M.26667j	M.15429	M.26654	M.22872	U.B.20189
Length head to distal epiphysis	—	48	63	59	43
Width proximal epiphysis	5·8	5·0+	7·0	6·5	4·6
Depth proximal epiphysis	9·0+	8·5	10·3	8·5+	8·5
Width at distal epiphysis	—	10·6	13·7	14·5	10·1
Depth at distal epiphysis	—	8·3+	7·9+	6·9	6·5
Width at centre of shaft	—	5·4+	7·5	7·1	4·3
Depth at centre of shaft	—	4·1	3·5	3·7	3·1

Ulna. Right and left ulnae were associated with skull 6404 : 44 but the shaft of the left ulna (M.26667e) is shattered and only the right ulna M.26667b could be prepared completely. The right ulna lacks the distal and olecranon epiphyses and also the proximal portion of the semilunar notch including the anconeal process. The bone is approximately equal in length to that of the extant Indian elephant. The proximal extremity is the stoutest part of the bone and the olecranon, even without the epiphysis, is larger than the olecranon plus epiphysis of the Indian elephant. On the posterolateral side of the semilunar notch is a large scar marking the insertion of the anconeous muscle. A coronoid process projects cranially on either side of the radial notch, the medial process being the larger. The ulnar tuberosity, located on the craniomedial side of the ulna and separated from the medial coronoid process by a large depression, is less well developed for the insertion of the *brachialis* muscle than is the equivalent tuberosity in the elephant.

The middle third of the ulna shaft is triangular in transverse section with cranial, medial and lateral faces but reverts to a pentagonal cross-section at the distal epiphysis. The interosseous ridge extends distally along the medial edge beneath the ulnar tuberosity but dies out at the proximal edge of the distal third of the shaft. Flat surfaces on the caudal aspect of the bone mark the areas of attachment of the *external pollicis longus, extensor communis* and *flexor digitorum profundus* muscles and the ligament humeroantibrachialis. These are all developed much as in the Indian elephant. The shaft is of similar length to that of the Indian elephant but is considerably deeper and wider.

TABLE 14

Ulna measurements

Parameter	*Prodeinotherium hobleyi*		*Elephas maximus*
	M.26667b	M.26667e	U.B.20189
Length from olecranon to distal epiphysis	61*	53*	63
Width olecranon	13·6	12·2	15·2
Depth olecranon below semilunar notch	11·7	12·2	13·2
Width semilunar notch	7·6	—	6·7
Width coronoid processes	19·4	—	15·4
Width distal end of shaft	11·8	10·9	12·2
Depth distal end of shaft	13·7	14·7	11·9
Width midpoint of shaft	8·4	—	6·3
Depth midpoint of shaft	7·0	—	6·3

Carpal bones. A small number of carpal bones have been collected from Gebel Zelten sites. MacInnes (1942) reported several carpals from Rusinga Island, Kenya, and these he attributed to *P. hobleyi.* Examination and comparison of the East African and Gebel Zelten material has revealed that only three of MacInnes' specimens may definitely be attributed to *Prodeinotherium*—an incomplete left cuneiform (M.21875), a right magnum (M.21877) and a left unciform (M.21882). These are redescribed with the Gebel Zelten material.

Cuneiform. The left cuneiform from Gebel Zelten (6405 : 98) is better preserved than that from Rusinga. The proximal surface that articulates with the ulna bears two articulation facets (a median rectangular facet and a lateral triangular facet) separated by a sagittal ridge. In *Elephas* and *Mastodon* the proximal articular surface of the cuneiform is saddle-shaped with a transverse depression through the centre. The distal surface of the deinothere cuneiform bears a triangular concavo-convex facet for articulation with the unciform, much as in the elephant or mastodon. On the caudal border there is a triangular facet for articulation with the pisiform, the hypoteneuse of the triangle being bounded by a deep groove extending down the large posterolateral process from the caudal junction of the proximal facets. The distal surface of the posterolateral process of the Gebel Zelten cuneiform is eroded but, as in *Elephas,* it bears a facet for articulation with the fifth metacarpal. The medial surface bears a cranial and (larger) distal facet for articulation with the lunar.

TABLE 15

Cuneiform measurements

Parameter	*P. hobleyi* 6405:98	*D. giganteum* (Höwenegg)	*M. angustidens* M.21874	*E. maximus* U.B.20189
Maximum length	8·5	15·6	8·6	7·9*
Maximum width	11·7	19·3	11·0+	11·1
Depth cranial face	4·8	9·3	5·0	4·6
Depth caudal face	5·0	8·1	5·3	5·1*
Length proximal facet	6·3	11·9	5·9	5·5*
Width proximal facet	9·1	14·7	8·4+	7·7
Length distal facet	7·1	14·8	8·2	6·5
Width distal facet	7·5	13·6	8·0	7·5
Length posterolateral process	3·6	7·0	4·0	3·9
Width posterolateral process	5·0	6·3	—	3·5
Depth posterolateral process	7·6	9·5	—	7·1

Lunar. An incomplete lunar (M.21876), identified by MacInnes (1942) as the left lunar of *Prodeinotherium hobleyi* is almost certainly mastodont. However the right lunar of both *P. hobleyi* and *Mastodon angustidens* are present in the collections of the Centre for Prehistory and Palaeontology, Nairobi. The *Prodeinotherium* lunar (KNM-RU 1291) is triangular and almost complete although the lateral edges are somewhat irregularly preserved. The facet articulating with the radius occupies nearly the whole of the proximal surface and extends nearly to the caudal edge of the bone. In contrast, that of *Mastodon* terminates more cranially. The radial facet is convex in the anteroexternal corner but concave over the remainder of the cranial surface. The ulnar facet at the anteroexternal corner is rhomboid and not triangular as in *Mastodon*. The magnum facet on the distal surface is convex cranially and concave caudally.

TABLE 16

Lunar measurements

Parameter	*P. hobleyi* KNM-RU1291	*D. giganteum* (Höwenegg)	*M. angustidens* KNM-RU 1260	*E. maximus* U.B. 20189
Maximum length	8·7	16·0	10·3	8·1
Maximum width	8·7	15·4	10·8	8·1
Maximum depth	5·8	10·8	7·1	5·3
Length radial facet	7·3	11·4	7·5	6·7
Width radial facet	7·3	13·6	8·5	6·0
Length magnum facet	7·7	13·9	9·0	7·1
Width magnum facet	8·0	13·4	8·6	7·2
Length ulnar facet	4·2	7·0	5·4	3·2
Width ulnar facet	3·5	4·3	4·0	2·9

Magnum. The right *Prodeinotherium* magnum from Rusinga (M.21877) is incompletely preserved but is more complete than a left magnum of *Mastodon angustidens* from Gebel Zelten (M.26652) that provides a basis for comparison. In *Prodeinotherium* the proximal surface of the magnum articulates with the lunar and is L-shaped, a postero-medial projection (the foot of the L) standing proud. In *Mastodon* or *Elephas* this projection merges gradually with the body and is relatively less distinct. The proximal facet of the deinothere magnum is divided into two portions—an almost flat cranial surface for articulation with the cranial part of the lunar and a convex caudal region that occludes with the caudal part of the lunar and scaphoid. The scaphoid articulates with the caudomedial projection of the magnum. The distal articular facet is pear-shaped (stem posterior) and concave for articulation with the third metacarpal. Four facets may be discerned on the medial side. The cranioproximal, craniodistal and caudoproximal facets are triangular and denote points of contact with the trapezoid. A mediodistal facet extends anteriorly beneath the craniodistal facet to articulate with the second metacarpal. The lateral side of the magnum adjoins the unciform and four facets may be observed. Two large proximal facets are separated by a central groove in contrast to the situation in the elephantoids in which the facets are contiguous. The distal unciform facets on the magnum are also separated, in contrast to the situation in *Elephas*, but the craniodistal facet is poorly developed as in *Mastodon*.

TABLE 17

Magnum measurements

Parameter	*P. hobleyi* M.21877	*D. giganteum* (Höwenegg)	*M. angustidens* M.26652	*E. maximus* U.B.20189
Maximum length	8·5	15·3	11·2	8·7
Width cranial edge	5·7	10·2	6·9	7·1
Width caudal edge	6·8	10·0	6·8	7·1
Depth cranial edge	5·7	10·4	6·7	6·2
Depth caudal edge	7·7	13·4	—	7·8
Length proximal facet	7·8	14·7	9·2	7·6
Width anterior edge proximal facet	4·7	9·9	6·6	7·1
Width posterior edge proximal facet	6·6	10·0	6·8	7·1
Length distal facet	6·8	14·0	—	6·7
Width distal facet	4·5	6·2	5·3+	4·5

Unciform. Three unciforms of *Mastodon angustidens* M.26653, M.26655, M.26657) are known from Gebel Zelten and contrast strongly in several features with the left *Prodeinotherium* unciform (M.21882); described by MacInnes (1942). In *Prodeinotherium*, the dorsal facet for articulation with the cuneiform is roughly triangular in outline. It reaches its maximum width at the anterior edge and tapers posteriorly. The cranial and caudal portions are convex but are separated by a transverse concave depression. The facet reaches its highest elevation at the caudomedial edge. The medial surface of the *Prodeinotherium* unciform bears a large proximal and two smaller distal facets for articulation with the magnum. Similar facets are also exhibited by *Elephas* and *Mastodon*. Three facets are apparent on the distal surface of the unciform. The medial facet is elongate, faces distomedially, is divided into two by a concave transverse groove and supports the lateral edge of the third metacarpal. The central facet is triangular (tapering posteriorly), is concave and articulates with the fourth metacarpal. It is separated from a larger rectangular, convex facet for Metacarpal V by a sagittal groove that is deepest posteriorly. Adjacent to the caudolateral edge of the McV facet but extending onto the proximal surface of the bone is a small, triangular, concave facet for the pisiform.

In the Gebel Zelten mastodont unciforms the cuneiform facet approximates to a rhomb and is longer than broad, the maximum breadth being achieved near the rear of the bone. In *Elephas* this facet is appreciably wider than long, the caudal edge being wider than the cranial, although the latter is relatively wider than in *Mastodon*. The distal facets of the Gebel Zelten mastodont unciforms are arranged much as in *Prodeinotherium* but are more elongate anteroposteriorly. These facets are of similar length in *Prodeinotherium* and the Indian elephant but in the latter the facets for McIV and McV are subequal in size and that for McIV is almost flat.

TABLE 18

Unciform measurements

Parameter	*P. hobleyi* M.21882	*D. giganteum* (Höwenegg)	*M. angustidens* M.26655	*E. maximus* U.B.20189
Maximum length	9·2	16·4	10·6	8·4
Maximum width	10·3	17·5	11·6	9·3
Maximum height	8·9	10·9	8·9	6·6
Length cuneiform facet	7·6	14·8	8·3	6·5
Width cuneiform facet	9·0	16·2	8·5	9·1
Length McV facet	6·8	8·9	6·5	5·9
Width McV facet	4·2	5·3	5·0	3·9
Length McIV facet	6·7	12·2	7·0	5·2
Width McIV facet	4·7	8·7	6·5	5·4
Length McIII facet	5·1	13·1	5·5	5·9
Width McIII facet	1·6	3·6	1·3	2·0

Pelvis. One half of a pelvis (M.26667g) was associated with the immature deinothere skeleton from Gebel Zelten site D. It may have belonged with the juvenile skull (6404 : 44), the adult skull (6404 : 14) or neither. Unfortunately the pelvis was shattered during transportation from the site.

Femur. A right *Prodeinotherium* femur (M.26667d) was associated with skull 6404 : 44. It lacks both the head and the distal epiphysis but the shaft is approximately the same length as that of the extant Indian elephant. The shaft is compressed craniocaudally and is virtually straight. The greater trochanter was developed much as in *Mastodon* or *Elephas*. The lesser trochanter is poorly preserved. The distal half of the cranial surface of the shaft bears a large ridge that becomes more swollen distally as it extends towards the patellar surface. This ridge is comparatively larger than in *Elephas* and suggests a larger area of attachment for the vastus intermedius muscle. The caudal surface of the *Prodeinotherium* femur, where preserved, strongly resembles that of the Indian elephant.

TABLE 19

Femur measurements

Parameter	*Prodeinotherium hobleyi* M.26667d	*Elephas maximus* U.B.20189
Length shaft	78·7	80
Width shaft at proximal epiphysis	25·5+	22·9
Depth shaft at proximal epiphysis	12·2+	10·7
Width shaft at distal epiphysis	20·8+	16·4
Depth shaft at distal epiphysis	17·6+	13·0
Width at centre of shaft	11·3	8·6
Depth at centre of shaft	9·6	6·5

Fibula. The distal third of the shaft of a *Prodeinotherium* fibula (M.26667a) was associated with skull 6404 : 44. The anterointernal border or interosseous ridge is separated from the anteroexternal border in the proximal half of the specimen by a narrow and flat anterior surface. The two borders converge in the distal half and the external border fades out before reaching the distal extremity. The posterior surface is round and broad but forms a sharp ridge immediately above the distal extremity. The lateral face is convex outwards and presumably served for the attachment of the *peroneous brevis* muscle. The medial face is concave and afforded attachment for the *flexor longus hallucis* muscle. From the distal epiphysis the bone decreases in width proximally, the change being gradual along the anterior edge but with a fairly sharp genuflexion along the posterior edge just below the dorsal limit of the specimen. From the shape of the posterior edge of the Gebel Zelten specimen it would seem that the bone was originally about as long as that of the Indian elephant. It differs from the latter, however, in that the distal extremity of the Gebel Zelten specimen is half as wide again.

Tarsal bones. MacInnes (1942) described an astragalus, two naviculars and an external cuneiform from Rusinga and attributed them to the taxon *Prodeinotherium hobleyi.* Comparison of the astragalus (M.21880) with mastodont astragali from Gebel Zelten and East Africa and with the astragalus facets of mastodont and deinothere tibiae confirms MacInnes' identification. The external cuneiform and navicular differ both in size and in some morphological features from the equivalent bones of the Indian elephant but are likely to have belonged to *Mastodon angustidens.*

Astragalus. The deinothere astragalus is more equant than that of *Mastodon.* The dorsal and medial surfaces bear a rectangular convex facet for articulation with the tibia. This facet is as long but less wide and more convex than that of *M. angustidens.* The anterior border of the *Prodeinotherium* astragalus from Rusinga is broken but the missing portion was probably of similar appearance to that of *Mastodon* except that the groove on the craniomedial surface, separating the tibial facet from the navicular facet, was less deep and less wide than in *Mastodon.* There are three facets on the distal surface—a triangular and convex navicular facet and two calcaneum facets. In *Prodeinotherium* the navicular facet extends to the craniomedial border of the astragalus, the medial edge of the facet being concave. The medial tip of the navicular facet of *Mastodon* is also concave but extends less far medially. The groove separating the navicular facet from the lateral calcaneal facet is deeper but less wide than in *Mastodon*. The lateral calcaneal facet is triangular and is flatter than that of *Mastodon*. The caudomedial calcaneum facet is oval and concave. It is separated from the lateral facet by the continuation of the same groove that separates the latter from the navicular facet. The medial calcaneal facet is separated from the navicular facet only by a very shallow groove and extends posteriorly onto the under surface of the massive posteromedial projection. On the lateral surface of the astragalus the facet for articulation with the fibula appears to be as long as, but much wider than, that of *Mastodon*.

Table 20

Astragalus measurements

Parameter	*P. hobleyi* M.21880	*D. giganteum* (Höwenegg)	*M. angustidens* M.26658	*E. maximus* U.B. 20189
Length lateral edge	7·9	—	7·4	7·4
Length medial edge	11·0	16·0	7·8+	10·2
Maximum width	10·9+	17·7	10·0*	11·5
Depth medial edge	7·1	9·5	7·1	7·9
Depth lateral edge	4·4	7·4	3·2	4·4
Length tibial facet	6·9	—	7·3+	6·9
Width tibial facet	7·3	—	8·3	8·3

Skeletal evidence on the locomotion of deinotheres The limb material of the Gebel Zelten deinotheres is too fragmentary to permit a detailed functional analysis. Nevertheless, comparison of these specimens with other *Prodeinotherium* and *Deinotherium* remains affords some information about the locomotion of these animals. The most important skeletal elements in this respect would appear to be the scapula, femur, manus and pes.

Smith and Savage (1956) determined that in graviportal mammals the scapula tends to be high and broad to afford sufficient surface area for the *serratus* and other shoulder muscles. They noted that the scapula blade of graviportal mammals is frequently expanded posteriorly to increase the mechanical advantage of the main retractor muscle of the forelimb (the *teres major*) and that the spine is usually heavy and may bear a posteriorly projecting flap in the region overlying the infraspinous fossa (*Rhinoceros*, *Brontops*). Alternatively the spine may end in a large acromion (*Loxodonta*, *Uintatherium*). The *trapezius* muscle originates on the spine and metacromion, the *deltoid* on the acromion. Both these muscles aid in abducting the forelimb.

Compared with the scapula of *Elephas maximus*, the scapula of *Prodeinotherium hobleyi* (text-fig. 14) is less tall (51 v 62 cm) and less broad (25 v 42 cm). The caudal angle is sited more dorsally above the head of the scapula (25 v 15 cm) and is less elongate posteroventrally from the spine (26 v 30 cm). Because the caudal angle of the scapula is sited more dorsally in *Prodeinotherium* than in *Elephas*, the mechanical advantage of the teres muscle is thereby decreased. Smith and Savage (1956) have shown that the mechanical advantage of the teres muscle is equivalent to the length of the moment arm of the teres muscle divided by the perpendicular distance from the glenoid to the ground. The mechanical advantage of the teres muscle of the Indian elephant is nearly 1/13 but that of *P. hobleyi* is 1/16.

The supraspinous fossa of *Prodeinotherium hobleyi* is relatively smaller than that of *Elephas*, and the scapular spine rises less abruptly and more dorsally. An acromion process is developed on the spine of the *P. hobleyi* scapula and is sited more dorsally than in *Elephas*. A metacromion is also present, sited level with the base of the acromion and forming a flap overhanging the infraspinous fossa. Both acromion and metacromion are reduced in comparison with those of the Indian elephant. Behind the metacromion the spine of *P. hobleyi* is broader and more robust than in the Indian elephant.

The supraspinous fossa of *D. giganteum* from Valladolid, Spain, is even more reduced than that of the Gebel Zelten deinothere. The caudal angle of the *Deinotherium* scapula is less posteroventrally produced than in the extant elephants and, significantly, there are no processes diverging from the relatively slender spine. The absence of acromion and metacromion was also noted by Stefanescu (1899) on the scapula of *D. 'gigantissimum'* from Manzati, Rumania. Reduction of the spine and supraspinous fossa, and the absence of acromion and metacromion would in artiodactyls be regarded as evidence of cursorial modification (Smith & Savage, 1956).

The retention of a rigid body axis is essential in animals of elephantine bulk in order to support the weight of the body. The method of rapid locomotion is thus limited to a fast amble or trot. The more rapid action of the teres muscle of deinotheres when taken in conjunction with other features of the scapula does, however, suggest that *Deinotherium* was potentially capable of more rapid locomotion than the elephantoids. Such an interpretation is supported by other features of the appendicular skeleton and tallies with Tobein's (1962) interpretation of the function of the *Deinotherium* manus and pes. *Prodeinotherium*, although more typically graviportal than *Deinotherium*, shows some signs of cursorial adaptation.

The humerus of the Gebel Zelten *Prodeinotherium* must have been slightly shorter than that of the Indian elephant but was still appreciably longer than the ulna. The shaft of the humerus is compressed laterally and elongated anteroposteriorly in direct contrast to the condition in *Elephas*. The lateral epicondyle is shorter than in *Elephas* but projects farther laterally. The condyles of the distal epiphysis have a greater degree of curvature in *Prodeinotherium* than in *Elephas* suggesting that the ulna of *P. hobleyi* may have been capable of being flexed through a greater angle.

The ulna of the Gebel Zelten deinothere is of similar length to that of the Indian elephant but is proportionately stouter. As in the elephantoids the nearly vertical alignment of the forelimb requires an olecranon process that diverges at right angles from the shaft. There is no evidence to suggest that the ulna was fused to the radius at its distal end although fusion at this point would seem likely. The distal epiphyses of both the ulna and radius were proportionately more massive in *Deinotherium* than in *Prodeinotherium*.

The radius of *Prodeinotherium* is best known from Maboko Island, Kenya, that from Gebel Zelten being represented only by the head. *Prodeinotherium* radius M.15429 is again about the size of that of *Elephas maximus*. It is less straight proximo-distally and craniocaudally than in the elephantoid proboscideans. The radial tuberosity is less well developed than in *Mastodon angustidens* and the interosseous ridge diverges halfway down the shaft. The radius shaft of both *Mastodon angustidens* and *P. hobleyi* is relatively wide laterally and compressed craniocaudally, but, whereas the mastodont shaft retains this shape throughout its length, that of *Prodeinotherium* becomes progressively more equant distally.

Only the large carpal bones of *Prodeinotherium* have been examined. These are serially arranged and are smaller but similar in shape to those of *D. giganteum* from Höwenegg, Germany (Tobein, 1962). The morphology of the proximal surface of the cuneiform suggests that the medial malleolus of the ulna extended farther distally in deinotheres than in elephantoids. No metacarpals have been collected from Gebel Zelten but a limited amount of information about the metacarpals may be gleaned from the distal row of carpal bones. In the unciform the facet for McV is proportionately larger and less laterally orientated than in the Höwenegg *Deinotherium* specimen and the facet for McIII is smaller. The magnum of *Prodeinotherium* bears a large facet for McIII and a smaller and more laterally aligned facet for McII.

Ehik (1930) described metacarpal fragments of *P. bacaricum* from Kotyhaza, Hungary. These were laterally compressed, but less so than the metacarpals of *Deinotherium giganteum* from Pikermi, Greece, described by Dietrich (1916). The metacarpals of *P. bavaricum* are less elongate than those of *D. giganteum* and resemble more closely those of *Elephas*. Whereas Dietrich (1916) and Tobein (1962) stated that the first metacarpal of *D. giganteum* is sufficiently reduced to suggest functional tetradactyly of the manus, Ehik alleges that in *P. bavaricum* the fifth metacarpal shows the greatest reduction. The distal articulation surface of the fourth metacarpal of *D. giganteum* is concave but that of *P. bavaricum* is concavoconvex. Ehik (1930 : 12) implies that the manus of *P. bavaricum* was more plantigrade than that of *D. giganteum*.

The metacarpals of *D. giganteum* are dolichopodous (Tobein, 1962). Whereas the proximal epiphysis of the fourth metacarpal of *D. giganteum* is orientated at right angles to the longitudinal axis of the shaft of the bone, the proximal epiphysis of McIV of *P. bavaricum* is aligned obliquely to the longitudinal axis of the shaft. The digits of *P. bavaricum* must therefore have spread farther laterally, were probably more uniform in size and are likely to have been less digitigrade than those of *D. giganteum*. The trapezium and trapezoid bones of *Prodeinotherium* have not been examined and it is therefore impossible to say if the first metacarpal was reduced as in *D. giganteum*.

The long bones of the hind limb of the deinotheres are similar in many respects to those of the elephantoids. The head of the femur is vertically aligned and, as in other graviportal mammals, the femur is longer than the tibia. Osborn (1929 : fig. 670) formulated the general rule that, relative to the length of the tibia, the femur of cursorial mammals shortens with increase in potential speed while the pes elements become more elongate. The femur and tibia of *Prodeinotherium* are of comparable lengths to those of *Elephas maximus* but the femur of *D. giganteum* from Valladolid is relatively shorter with respect to the tibial length. The tibia/femur ratio of *E. maximus* is 0·55 whereas that of *D. giganteum* is 0·71, indicating that the femur of

D. giganteum is about 30% shorter than that of the extant Indian elephant. Reduction of the first metatarsal in *Deinotherium* was noted by de Pauw (1908), and the narrow elongate pes of *D. giganteum* in conjunction with the dolichopody of the digits convinced Tobein (1962) that *D. giganteum* was capable of swifter locomotion than its contemporary elephantoids. The reduction in length of the *Deinotherium* femur would appear to support Tobein's interpretation.

The equant tibial facet of the astragalus of all deinothere taxa from which this bone is known is a distinctive character that reflects the comparatively narrow width of the pes of deinotheres compared to that of elephantoids. The tibial facet of *Prodeinotherium* astragali is more convex than in astragali of its contemporary elephantoids but that of *Deinotherium* is flatter. The large posteromedial projection from the *Prodeinotherium* astragalus is not present in either *Mastodon* or *Elephas* and is reduced in *Deinotherium*. The surfaces of the *Prodeinotherium* astragalus that articulate with the fibula and medial malleolus of the tibia are larger and more vertically orientated than in *Mastodon angustidens*.

IV. CONCLUSIONS

The family Deinotheriidae is known from Africa, Europe and western Asia. All representatives of this family are large. Features of the skull and dentition serve to distinguish the deinotheres from the elephantoids and distinctive characters may also be seen in the postcranial skeleton. On their dental characters the deinotheres appear to be most closely related to the barytheres and moeritheres and may have been derived from ancestral *Barytherium* stock during the early Tertiary.

The family Deinotheriidae is represented by two genera, the primitive *Prodeinotherium* and the later and larger *Deinotherium*. The Gebel Zelten specimens are assigned to *Prodeinotherium hobleyi*. They include the earliest deinothere skulls yet recovered and the fine condition of preservation of the skulls permits their use for reinterpreting the morphology of less well preserved *Deinotherium* skulls. The Gebel Zelten specimens exhibit a number of primitive deinothere features including a steeply downturned rostrum, narrow and more anterior external nares, a skull roof that is proportionately wider and longer, less elevated occipital condyles, shorter paroccipital processes and a more vertically inclined occiput.

The facial region of *P. hobleyi* was modified for the attachment of a proboscis as was that of *Deinotherium*. The cranial region was adapted for greater movement of the skull on and with the neck than in elephantoids. The most important modifications enlarge the paroccipital processes and elevate the occipital condyles to increase the downward thrust of the mandibular tusks. Reversed curvature of the zygapophyses of the cervical vertebrae (compared to that of elephantoids) also aids in the downward movement of the head.

In detail the dental characters render the deinotheres unique. Loss of the superior pre-cheek teeth and retention of a single pair of downturned inferior tusks is a combination not exhibited by any other mammal. The main function of the tusks may have been for self defence and feeding, both involving a violent downward thrust of the head. It would seem unlikely that the tusks were used for digging and their main function in feeding was probably for clearing and stripping vegetation. Wear facets on the anteromedial surface of the tusk tip in a number of deinothere tusks would appear to support this interpretation. Lophodont cheek teeth have been evolved in several mammalian groups but the trilophodont anterior molars of the deinotheres are unique. The deciduous fourth premolar is also trilophodont and served as a shearing tooth in contrast to the crushing function of the second and third milk premolars. The anterior permanent molar initially serves as a shearing tooth but after the posterior molars have been erupted it becomes part of the anterior crushing battery. The second and third molars are bilophodont and persist as shearing teeth until the lophs are removed by wear. The angle of shear changes from nearly vertical in newly erupted teeth to almost horizontal in greatly worn teeth. The shearing surface is maintained by thegosis. There is no increase in hypsodonty or brachyodonty throughout the recorded history of the deinotheres, and the length versus width parameters of the teeth of all deinotheriid taxa remain constant.

Deinothere vertebrae are unfortunately rare but the axis and atlas vertebrae are known. They may readily be distinguished from those of the elephantoids and are modified to provide large attachment areas for the muscles of the neck. The zygapophyses of the cervical vertebrae have reversed curvature relative to those of the elephantoids. The neural spines of the anterior thoracic vertebrae were apparently longer and more posteriorly inclined than those of contemporary elephantoids. Differences from elephantoid structure may also be seen in the appendicular skeleton, the scapula and foot bones being most distinctive, the long bones less so. Advanced characters shown by *Deinotherium* include reduction of the scapular spine, elongation of the carpals, tarsals and metapodials, elevation in posture of the manus and pes and reduction of the first digit leading to the functional tetradactyly of the feet. Many of the limb modifications point to a cursorial adaptation of *Deinotherium*, but *Prodeinotherium* resembles *Elephas* in the size and proportions of the long bones.

Prodeinotherium and *Deinotherium* are separated on the basis of size, minor modifications of the dentition and characters of the skull and postcranial skeleton. Six species are recognized: *P. hobleyi*, *P. bavaricum*, *P. pentapotamiae*, *D. giganteum*, *D. indicum* and *D. bozasi*. Each species is based primarily on geographic distribution. The conservative dental characters of deinotheres are of little use for specific differentiation but the skulls and skeletal elements may prove more diagnostic when these are better known.

Deinotheres must have originated in Africa during the early Tertiary but are first known from the early Miocene. During the early Miocene *Prodeinotherium* migrated from Africa via the Middle East (and perhaps the western Mediterranean) into Eurasia. By the late Miocene *Deinotherium* had appeared. Possibly two species evolved separately, *D. giganteum* from *P. bavaricum* in Western Europe and *D. indicum* from *P. pentapotamiae* in western Asia. More probably *Deinotherium* was derived from *P. bavaricum* and then spread eastwards. *Deinotherium* and *Prodeinotherium* coexisted in Eurasia during the late Miocene. *Prodeinotherium* had become extinct in Eurasia by the end of the early Pliocene and *Deinotherium* by the middle Pliocene.

P. hobleyi was present in East and North Africa during the early Miocene but was thereafter restricted to East Africa. It survived into the Pliocene but is not known to have coexisted with *D. bozasi* which had appeared by the beginning of the Pleistocene. Whether *D. bozasi* evolved *in situ* or represented the southerly migration of the Eurasian deinotheres cannot yet be determined but the former seems more likely in view of the limited distribution of African deinotheres after the early Miocene.

Both *Prodeinotherium* and *Deinotherium* were browsing mammals that used their tusks and probosces to gather food. The proboscis of *Prodeinotherium* was smaller, and the skeleton lacked many of the cursorial adaptations of *Deinotherium*. *Prodeinotherium* probably inhabited more densely vegetated regions while *Deinotherium* frequented more open territory. There is no obvious successor to *Deinotherium* in the middle or late Pleistocene of Africa. Whether it failed to adapt to changing environmental conditions or was supplanted through competition from a group or groups of smaller herbivorous mammals must remain a matter for conjecture.

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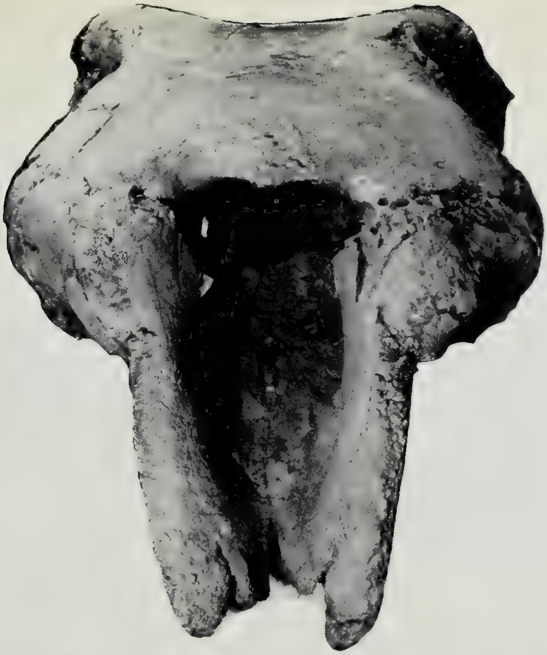
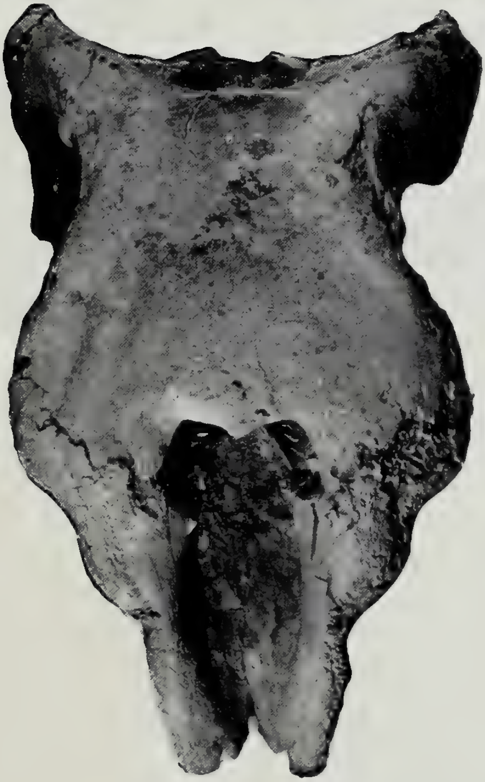
PLATE 1

Fig. a. ***Prodeinotherium hobleyi*** skull (M.26665), anterior view.

Fig. b. ***Prodeinotherium hobleyi*** skull (M.26665), dorsal view.



1a

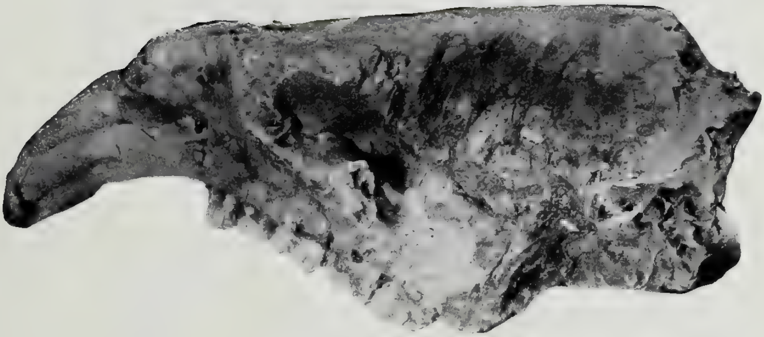


1b

PLATE 2

Fig. a. ***Prodeinotherium hobleyi*** skull (M.26665), left lateral view.

Fig. b. ***Prodeinotherium hobleyi*** skull (M.26665), right lateral view.



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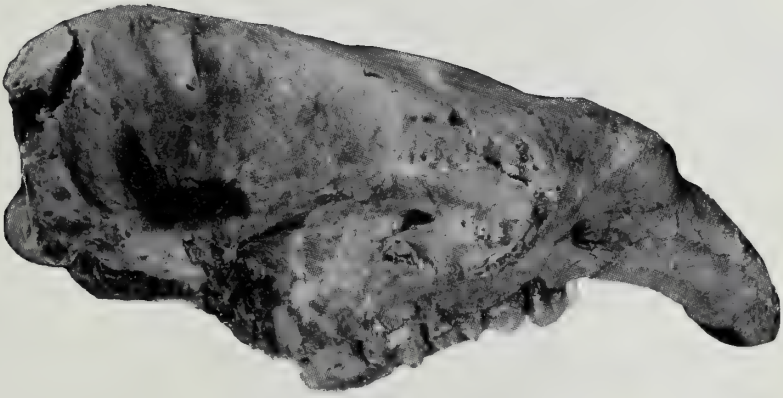
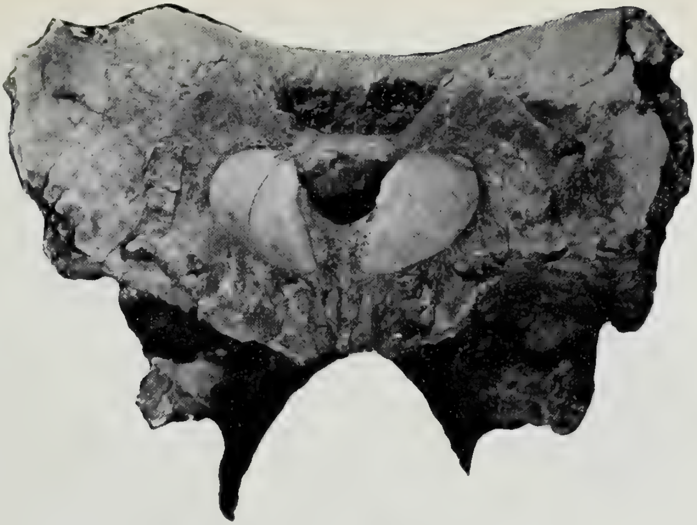


2b

PLATE 3

Fig. a. ***Prodeinotherium hobleyi*** skull (M.26665), posterior view.

Fig. b. ***Prodeinotherium hobleyi*** skull (M.26665), ventral view.



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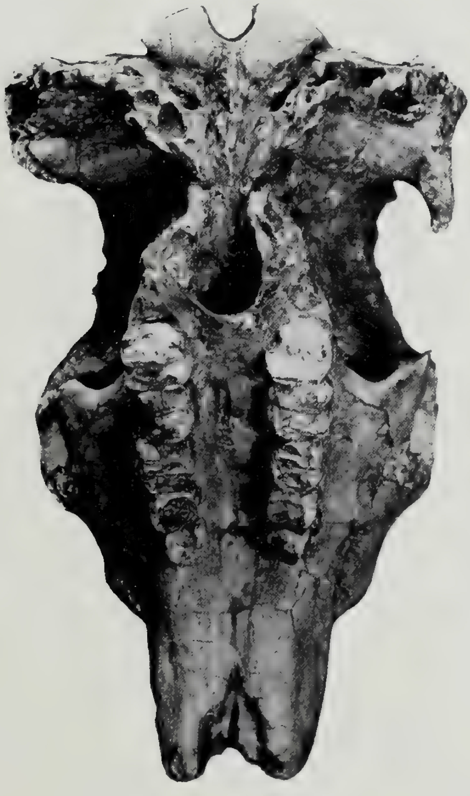
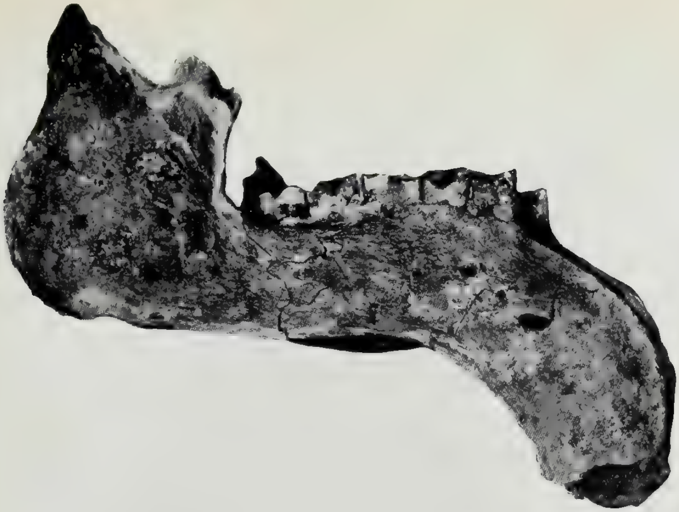


3b

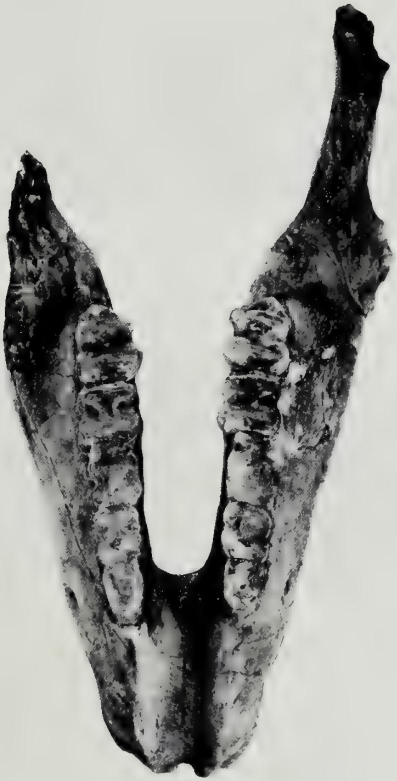
PLATE 4

FIG. a. ***Prodeinotherium hobleyi*** mandible (6412 : 10), right lateral view.

FIG. b. ***Prodeinotherium hobleyi*** mandible (6412 : 10), dorsal view.



4a

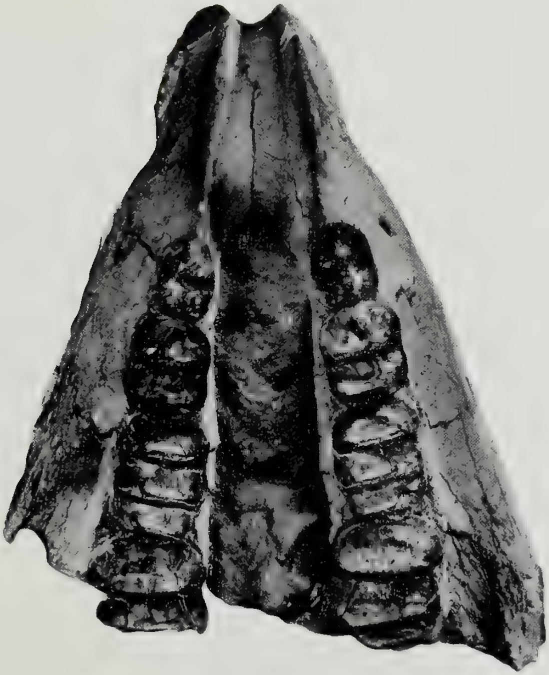


4b

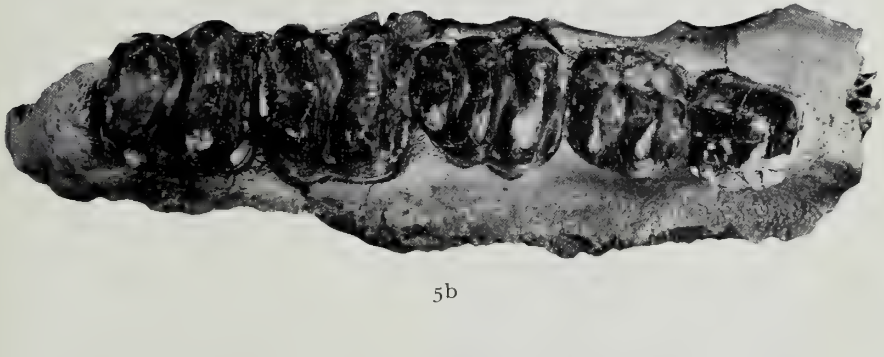
PLATE 5

FIG. a. ***Prodeinotherium hobleyi*** mandible (6404 : 13), dorsal view.

FIG. b. ***Prodeinotherium hobleyi*** right maxilla (6401 : 4) ventral view.



5a



5b

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- 4 OCT 1973
NATURAL HISTORY

CIRRIPEDES FROM THE UPPER CRETACEOUS OF ALABAMA AND MISSISSIPPI, EASTERN GULF REGION, U.S.A.

I. PALAEONTOLOGY

J. S. H. COLLINS

II. GEOLOGY

F. F. MELLEN

BULLETIN OF
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GEOLOGY Vol. 23 No. 6
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I. PALAEONTOLOGY

BY
JOSEPH STEPHEN HENRY COLLINS
Dulwich, London

Pp 349–380; 5 *Plates*, 3 *Text-figures*

II. GEOLOGY

BY
FREDERIC FRANCIS MELLEN
Jackson, Mississippi, U.S.A.

Pp 381–388; 2 *Text-figures*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 23 No. 6
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TRUSTEES OF
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CIRRIPEDES FROM THE UPPER CRETACEOUS OF ALABAMA AND MISSISSIPPI, EASTERN GULF REGION, U.S.A.

PART I. PALAEONTOLOGY

By J. S. H. COLLINS

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SYNOPSIS

From the Upper Cretaceous Selma Chalk and Ripley Formation of Mississippi and Selma Chalk of Alabama, U.S.A. valves of nine new species and one new subspecies of cirripedes are described and figured: *Cretiscalpellum harnedi, C. macrum, C. vallum, C. venustum, Arcoscalpellum bakeri, A. campus, A. hubrichti, A. withersi, Brachylepas angulosa, Virgiscalpellum gabbi apertus.* Further valves belonging to *Virgiscalpellum gabbi* (Pilsbry) and two other *Virgiscalpellum* valves are described and figured from the Ripley Formation. They occur in silty, finely sandy and highly foraminiferal and ostracodal horizons within the 'Selma' which represents an 'outer neritic' environment of the continental shelf. Three biostratigraphic horizons are recognized: (1) zone of *Virgiscalpellum* of Ripley and basal Prairie Bluff (Maastrichtian) age; (2) zone of *Cretiscalpellum vallum* of basal Annona or upper Coffee (Campanian) age; and (3) zone of *Arcoscalpellum hubrichti* of middle Mooreville (Santonian) age. These three zones supplement known faunal zones within the Upper Cretaceous.

INTRODUCTION

BETWEEN 1935 and 1938 F. F. Mellen corresponded with T. H. Withers of the British Museum (Natural History) and sent numerous small collections of cirripede valves to him for study and for description in a paper Withers had planned. The new forms recognized were received too late for inclusion in the monographic *Catalogue of Fossil Cirripedia*, Vol. 2, *Cretaceous*, 1935. The holotypes were to be retained in the British Museum (N.H.) and paratypes were to be returned to the Department of Geology and Geography at Mississippi State University.

The intervention of World War II, the retirement of Withers and his death in 1958, prevented the completion of the study of the Mississippi barnacle collections which, according to present tabulation, numbered 146 valves from seven localities (see below).

Bull. Br. Mus. nat. Hist. (Geol.) **23**, 6

Between 1967–1969 many valves were secured from previous collections and additional hundreds were collected by F. F. Mellen and others, not only from those of the earlier sites that still existed, but from new localities scattered over several Counties in Alabama and Mississippi. A further group of 36 valves, from Greene County, Alabama, were lent to J. S. H. Collins by the Paleontological Research Institute, Ithaca, New York.

HISTORICAL REVIEW

The present material contains only one, *Virgiscalpellum gabbi* (Pilsbry), of the eight species of cirripedes previously recorded from the Cretaceous of the United States of America. Of the other seven species, the generic position of one, *'Scalpellum' inaequiplicatum* Shumard 1862, from the Upper Senonian of Texas, was considered by both Shumard and Withers (1935) as provisional, owing to the poor preservation of the specimen. The inadequate description of *Scalpellum* sp. listed by Adkins 1928, from the Upper Austin Chalk of Texas, was also considered to be equivocal by Withers (1935). Of the remaining species, *Loriculina ?texanum* Withers is recorded from the Middle Albian of Texas; *Calantica* (*Titanolepas*) *martini* Withers, *Stramentum haworthi* (Williston) and *Squama spissa* Logan are known from the Senonian of Kansas. *Stramentum canadensis* (Whiteaves) (Withers, 1935) has been described from the Fort Benton group of Manitoba and recently Russell (1967) added a further Canadian species, *?Calantica saskatchewanensis*, from the Bearpaw Formation of southwestern Saskatchewan. *Arcoscalpellum conradi* (Gabb, 1876) from the Vincentown Formation of New Jersey, must now be regarded as a Palaeocene form (Richards, 1958), which substantiates Withers' (1935) opinion that the scutum and carina of this resembled certain Tertiary species.

Students and collectors of the rich fauna of Upper Cretaceous sediments of Mississippi, Alabama and Tennessee made great use of Wade (1926) in the identification of fossils, despite its limitation to basal Ripley strata of Coon Creek, McNairy County, Tennessee. It was soon recognized that *Virgiscalpellum gabbi*, first recorded from Coon Creek, was present in the Ripley strata of Oktibbeha County, Mississippi, and that other barnacle types were also present.

The collections to be considered afford an aggregate of some 1493 valves; from these 46 different valves have been distinguished and are included in the following species:

Cretiscalpellum harnedi sp. nov.
    C. macrum sp. nov.
    C. vallum sp. nov.
    C. venustum sp. nov.
Arcoscalpellum bakeri sp. nov.
    A. campus sp. nov.
    A. hubrichti sp. nov.
    A. withersi sp. nov.
Virgiscalpellum gabbi gabbi (Pilsbry)
    V. gabbi apertus ssp. nov.
    V. sp.
    V. sp.
Brachylepas angulosa sp. nov.

This material not only allows nine new species and one new subspecies to be described, but also includes the first member of the sub-order Brachylepadomorpha to be recorded from the Western Hemisphere. The new material of *V. gabbi* allows us to add the scutum, tergum, carinal and rostral latera to the known valves of that species. Moreover, these valves show that *V. g. gabbi* is related to the Maastrichtian species *V. hagenowianum* (Bosquet) which occurs only at Maastricht.

Both Pilsbry (1933) and Withers expressed doubts whether or not the upper latus, figured by Withers (1935, p. 39, fig. 2, erroneously called a scutum by Wade, 1926) should be ascribed to *V. gabbi*. In his notes on the valves present in the original collections sent to the British Museum (Nat. Hist.), Withers had considered that this valve really belonged to the species here named *A. withersi* but in view of the additional material in the present collections, which bear a striking similarity to the upper latus of *V. darwinianum* (Bosquet) figured by Withers (1935, pl. 38, fig. 1) there seems little to support this opinion. Until such time as more material becomes available, these particular upper latera are here retained, with reservation, in *V.g. gabbi*. The present material from the Ripley Formation of Mississippi shows that the carina of *V. gabbi* is very variable in structure and carinae similar to the one Withers set aside in his notes as a new species are here regarded as a subspecies of *V. gabbi*. Also, a distinct scutum and tergum ostensibly from the Ripley Formation and Annona chalk respectively are described, but not named. These anomalies indicate that much remains to be learned of the genus *Virgiscalpellum*, particularly from the American Cretaceous. It is felt that extensive new collections are desirable to allow a re-study of the genus to be made.

The valves of *Arcoscalpellum hubrichti* have characters in common with both of the European Groups of *A. maximum* (J. de C. Sowerby) and *A. fossula* (Darwin); both *A. campus* and *A. withersi* have affinities with the Group of *A. fossula*.

Of the four species of *Cretiscalpellum* present, *C. vallum* is the best known; not only is it represented by numerous carinae, but also by eight other different valves. *C. macrum* and *C. venustum*, the geologically oldest species of the genus in the present collection, are known from only fifteen and four valves respectively, while *C. harnedi*, the youngest of the genus in this study, is represented by thirteen valves.

Withers (1927, 1935, 1953) and Cheetham (1963) have fully discussed the morphology and classification of fossil lepadomorph cirripedes and the latter has also provided a comprehensive survey of North American Tertiary species.

Following the practice adopted by Darwin, a carina, when present, has been selected as holotype.

ABBREVIATIONS

The following abbreviations relating to Museum and other collections have been used in the text: BMNH, British Museum (Natural History); MSU, Mississippi State University; PRI, Paleontological Research Institution.

SYSTEMATIC DESCRIPTIONS

Series Cirripedia Burmeister, 1834

Order THORACICA Darwin, 1851

Suborder LEPADOMORPHA Pilsbry, 1907

Family **SCALPELLIDAE** Pilsbry, 1916

Genus ***CRETISCALPELLUM*** Withers

1922 *Cretiscalpellum Withers* : (9), 9, 374.
1935 *Cretiscalpellum* Withers : 2, 144.

Diagnosis: Scalpellidae with seventeen valves including four pairs of large and little differentiated, much overlapping lower latera; subcarina much larger than rostrum; carina with umbo apical.

Type species: *C. unguis* (J. de C. Sowerby).

Range: Aptian (Lower Greensand) to Maastrichtian.

Cretiscalpellum macrum sp. nov.

(Plate 1, Figs 1–6)

Diagnosis: Carina thin, moderately arched with fine apico-basal ridge, acute basal angle. Tergum and scutum thin, tergum with carinal margin divided into upper and lower portions.

Holotype: A carina. BMNH In.64414. (Pl. 1, fig. 1), Upper Senonian, Mooreville Chalk; 3 miles E. of West Greene and 3 miles W. of Clinton, Greene County, Alabama.

Material: 15 valves:

British Museum

In.64414.	Carina.	Holotype.	Pl. 1, fig. 1.	A5.
In.64415.	Scutum.	Paratype.	Pl. 1, fig. 3.	A1.
In.64416.	Tergum.	,,	Pl. 1, fig. 4.	A4.
In.64417.	Tergum.	,,	Pl. 1, fig. 6.	A8.

Mississippi State University

1311.	Carina.	Paratype.	Pl. 1, fig. 2.	A8.
1312.	Tergum.	,,	Pl. 1, fig. 5.	A8.
1339–45.	7 Terga.	Paratypes.		

LOCALITIES: Type locality, 3 miles E. of West Greene and 3 miles W. of Clinton, c. ¼ mile N.E. of church, c. Centre SW¼ Sec. 31, T. 23 N., R.1 E., Greene County, Alabama. Other localities—Al; A4; A6; A7; A8. Horizon: Mooreville Chalk, Upper Senonian.

DESCRIPTION: *Carina* (Pl. 1, figs 1–2) length about three times the width; it is thin and a little bowed inwards, the lateral margins are straight or slightly hollowed. The basal angle is acute (c. 60°) and the growth lines are directed downwards at the lateral edges to produce a weak spur. The tectum, with a fine, slightly beaded apico-basal ridge, is broadly arched transversely, becoming slightly rounded and thickened at the sides. Fine longitudinal ridges, more prominent towards the side of the valve, make up the surface ornament. The inner surface is regularly concave and a thin ridge extends the length of the lateral margin.

Scutum (Pl. 1, fig. 3) thin and trapezoidal in outline, the width being about two thirds of the length. It is moderately convex transversely with a thin, sharp apico-basal ridge, another ridge of equal prominence passes from the apex to half way along the basal margin. The basal margin is moderately convex, it forms an angle of about 80° with the apex on the occludent side and nearly a right angle with the lateral margin. The occludent margin is evenly rounded and the apex is directed towards the tergum. The tergal margin is concave and thickened at the apex. The lateral margin is rounded and shorter than the tergal margin. The tergo- and basi-lateral angles are sharp. On the inner surface near the occludent side and above the adductor muscle pit there is a deep depression which overhangs on the tergal side. A groove extends a short way along the inner occludent and tergal sides.

Tergum (Pl. 1, figs 4–6) thin and sub-quadrate in outline; the length is about twice the width. A fine apico-basal ridge, steep on the carinal side, divides the valve slightly to the carinal side of the midline. Two folds, extend from the apex to the scutal margin; the lower fold reaching the edge about half way along and the upper fold about midway between this and the scutal angle. The two areas enclosed by the ridges bounding these folds and the occludent margin are flat. The occludent margin is straight and equal in length to the scutal margin, which is concave where the folds reach the edge and convex to the base. The scutal and carinal angles are sharp. The carinal margin is divided into two almost straight portions; the upper portion is about half the length of the lower. The surface is smooth or ornamented with fine longitudinal ridges. On the inner surface a short groove extends along the occludent and carinal edges and growth lines form a slightly overhanging slip at the apex. The reverse of the folds on the outer occludent side is plainly discernable.

DISCUSSION: The carina may be readily distinguished from *C. venustum* by the rounded transverse section, the more obtuse angle of the basal margin and the thin, not rolled under, lateral margins. It differs from the later *C. harnedi* by the fine apico-basal ridge and sparser ornament. The nearest European species would appear to be *C. glabrum* (Roemer); the carina of *C. macrum* however, is much thinner, less arched transversely and has a much weaker apico-basal ridge, and the terga have two folds extending from the apex to the scutal margin.

The name of this species is derived from *macer*, thin.

Cretiscalpellum venustum sp. nov.

(Plate 1, Figs 7–9, 13)

DIAGNOSIS: Carina with tectum strongly arched and with weakly developed parietes directed a little inwards and thickened; the apico-basal ridge is rounded and the basal margin is nearly straight.

HOLOTYPE: A carina. BMNH In.64418 (Pl. 1, fig. *7a-b*), Upper Senonian, lower or middle Mooreville Chalk, Mt. Olive Church, Greene County, Alabama.

MATERIAL: 4 valves:

BRITISH MUSEUM

In.64418.	Carina.	Holotype.	Pl. 1, figs *7a-b*.	A7
In.64419.	Tergum.	Paratype.	Pl. 1, fig. 9.	A8

MISSISSIPPI STATE UNIVERSITY

1313.	Carina.	Paratype.	Pl. 1, fig. 8.	A8
1346.	Carina.	,,		A6

LOCALITIES: Type-locality, 1·2 miles due E. of Mt. Olive Church and in SW¼ of SW¼ Sec. 32, T.22 N., R.1 E., Greene County, Alabama. Other localities—A6; A8.

HORIZON: Lower or middle Mooreville Chalk, Upper Senonian.

DESCRIPTION: *Carina* (Pl. 1, figs 7, 9, 13) length approximately three times the width, nearly straight or a little bowed outwards, the sides being straight. The apex is acute and the basal angle is very wide (c. 120°). The tectum is strongly arched transversely and rounded at the lateral margins to form very weak parietes which are slightly rolled under to form a narrow ridge. Several rather prominent ridges extend along either side of the rounded apico-basal ridge; where this and the ridges forming the ornament are interrupted by the growth lines, they tend to be raised into low nodes. The inner surface is open to the apex and is evenly rounded.

Tergum (Pl. 1, fig. 9) rhomboidal in outline, the width being rather more than half the length. The apico-basal ridge is straight, steeper on the carinal side and situated slightly towards the carinal side of the midline. Two prominent folds extend from the apex to the scutal margin parallel to the occludent margin. The area between the apico-basal ridge and the lower fold is flat; the carinal side of the valve is flatly depressed. The occludent margin is straight and about as long as the scutal margin which is somewhat sinuous. The upper portion of the carinal margin is concave and shorter than the nearly straight lower portion which is about as long as the occludent margin. The carinal angle is sharp. The apico-basal ridge is slightly notched by growth lines and the surface is ornamented by numerous fine ridges distributed more or less evenly over the surface. On the inner surface very faint growth lines extend from the apex along the occludent and upper carinal edges. The reverse of the folds on the outer occludent side and a groove corresponding to the apico-basal ridge are prominent.

DISCUSSION: The carina of *C. venustum* is distinct from the other *Cretiscalpellum* species in the present collection. It has in the steep transverse section and the tendency for the intersection of the growth lines and longitudinal ridges to become beaded some affinity to the European species *C. striatum* (Darwin), but in the latter the parietes are stronger and not rolled under as in *C. venustum*.

The name of this species is derived from *venustus*—beautiful—in reference to the beaded ornament. *Cretiscalpellum* remains from the Mooreville Chalk appear to be quite rare, particularly when compared with the many hundreds of valves of *Arcoscalpellum hubrichti* that have been collected. The numerical ratio of *Arcoscalpellum* to *Cretiscalpellum* in these outcrops is approximately 200 : 1. With the accumulation of more material, it may well be found necessary to re-assess the specific identities of the scutum and terga here attributed to *C. macrum* and *C. venustum*.

Cretiscalpellum harnedi sp. nov.

(Plate 1, Figs 10–12)

DIAGNOSIS: Carina obscurely carinated, not divided off into parietes or intraparietes.

HOLOTYPE: A carina BMNH In.64421 (Pl. 1, figs 11*a-c*), Maastrichtian, Middle Ripley Formation, 1·5 miles E. of State College, Oktibbeha County, Mississippi.

MATERIAL: 13 valves:

BRITISH MUSEUM				
In.64420.	Scutum.	Paratype.	Pl. 1, figs 10*a-b*.	M8
In.64421.	Carina	Holotype.	Pl. 1, figs 11*a-c*.	M3
In.64422.	Tergum.	Paratype.	Pl. 1, fig. 12.	M8
In.64486.	Carina.	,,		M8
MISSISSIPPI STATE UNIVERSITY				
1314.	Carina	Paratype		OC.2
1315.	Tergum.	,,		M8
1347–51.	5 Carinae	Paratypes.		
1352–53.	2 terga	,,		

LOCALITIES: Type locality, 1·5 miles E. of State College: probably N.W. corner of NE¼ of NW¼ Sec. 6, T.18 N., R.15 E., Oktibbeha County, Mississippi. Other localities—OC.1; OC.2; M2; M3; M8.

HORIZON: Ripley Formation, Maastrichtian.

DESCRIPTION: *Carina* (Pl. 1, fig. 11) length is from twice to three times the width; it is slightly bowed inwards and strongly arched transversely with an obscure, flatly rounded median keel; it is not divided off into parietes or intraparietes. The apex is blunt and the basal margin is obtusely angular, forming an angle of about 120°; the basi-lateral angle is narrowly rounded. The outer surface is ornamented with fine longitudinal ridges. The inner surface is deeply concave and the apex is open to the top, indicating that little or none of the valve projected freely.

Scutum (Pl. 1, fig. 10) trapezoidal in outline and slightly concave longitudinally.

The occludent margin is straight and the apex is not directed towards the tergum. The tergal margin is straight and shorter than the slightly concave lateral margin. The apico-basal ridge and another passing to the basal margin is straight and flatly rounded. A number of fine ridges, rather more numerous on the occludent side, make up the surface ornament. On the inner surface a slight groove above the adductor muscle pit extends towards the apex.

Tergum (Pl. 1, fig. 12) similar to that of *C. macrum*, but it is thicker and more elevated transversely. The apico-basal ridge is much rounded, steep on the carinal side and hardly at all raised on the occludent side. The occludent margin is thickened and raised to form a low ridge. The folds extending from the apex to the scutal margin are hollowed and bounded on the carinal side by broadly rounded ridges.

DISCUSSION: Differences with *C. macrum* have been discussed above. The arched carina readily distinguishes it from that of *C. vallum*. The apico-basal ridge of the tergum is somewhat stronger and more rounded than that of *C. vallum*, and the folds on the occludent side are regular and more evenly spaced. Compared with *C. vallum*, the ridges on the scutum are sharper and the outer surface is not so strongly ornamented. In dorsal view the carina somewhat resembles *C. subcarinatum* Withers (1935, pl. 18, figs 12, 15), but this species has narrow parietes set abruptly inwards.

The species is named after the brothers Horace H. Harned, Jr., and Wentworth V. Harned, who contributed much of the material used in this work.

Cretiscalpellum vallum sp. nov.

(Plate 1, Figs 14–22; Plate 2, Figs 1–12; Text-fig. 1)

DIAGNOSIS: Carinal margins produced to narrow wall-like parietes; portions of tectum on either side of the apico-basal ridge depressed; the other valves with well developed apico-basal ridge.

HOLOTYPE: A carina. BMNH In.64423 (Pl. 1, figs 15*a-b*, 17*a-b*). Upper Senonian, basal Annona or upper Coffee Formation, Tibbee Creek, Clay County, Mississippi.

MATERIAL: 168 valves:

BRITISH MUSEUM

In.64423.	Carina.	Holotype.	Pl. 1, figs. 15*a-b*, 17*a-b*	M11
In.64424.	Subcarina.	Paratype.	Pl. 1, figs 22*a-b*.	M11
In.64425.	Scutum.	,,	Pl. 1, figs 20*a-b*.	M11
In.64426.	Tergum.	,,	Pl. 1, fig. 18.	M11
In.64427.	Upper latus.	,,	Pl. 2, fig. 11.	M11
In.64428.	Tergum.	,,	Pl. 2, figs 2*a-b*.	M11
In.64429.	Rostral latus.	,,	Pl. 2, fig. 7.	M11
In.64430.	Subcarinal latus.	,,	Pl. 2, fig. 8.	M11
In.64431.	Inframedian latus.	,,	Pl. 2, fig. 9.	A10
In.64432.	Upper latus.	,,	Pl. 2, fig. 10.	OC.6
In.64433–4.	2 Carinal latera.	,,	Pl. 2, figs 5–6.	M11
In.64435.	Tergum with small bivalve.	,,	Pl. 2, fig. 3.	M11

In.64482.	Carina with small bivalve.	,,		M11
In.64483.	Subrostrum.	,,	Pl. 2, fig. 12.	M11
In.64484.	Carina.	,,		M11
In.64485.	Scutum	,,		M11

MISSISSIPPI STATE UNIVERSITY

1316.	Carina.	Paratype.	Pl. 1, figs 14*a-b*.	M11
1317.	Scutum.	,,	Pl. 1, fig. 19	M11
1318.	Tergum.	,,	Pl. 2, fig. 4.	M11
1319.	Upper latus.	,,	Pl. 1, fig. 21.	M11
1320.	Subcarina.	,,	Pl. 2, fig. 1.	M11
1321.	Carinal latus.	,,		M11
1354.	Sub-carinal latus.	,,		M11
1355.	Carina with small bivalve.	,,	Pl. 1, fig. 16.	M11
1427.	Scutum.	,,		M11
1428.	Tergum.	,,		M11
	26 Carinae.			
	21 Scuta.			
	86 Terga.			
	1 Upper latus.			
	6 Carinal latera.			
	1 Subcarina.			

LOCALITIES: Type locality, $4\frac{1}{2}$ miles S. of West Point, south valley wall of Tibbee Creek, E. of U.S. Highway 45-W, NE$\frac{1}{4}$ of SE$\frac{1}{4}$ Sec. 6, T.19 N., R.16 E., Clay County, Mississippi. Other localities—A10.

HORIZON: Basal Annona or upper Coffee Formation, Upper Senonian.

DESCRIPTION: *Carina* (Pl. 1, figs 14–17) thin; approximately three times as long as wide. It is straight or very slightly bowed inwards in typical forms, but sometimes a little recurved at the apex. The median portion of the tectum is raised, rounded and topped by a thin apico-basal ridge; on either side of the rounded portion the tectum is flat or concave to the margin which is rounded and produced inward to form narrow wall-like parietes. The basal angle is sharp, c. 85°, the basal margins are slightly excavated and produced into a thin spur at each basi-lateral angle. The growth lines are raised into low ridges and fine apico-basal ridges are usually developed. On the inner surface the lower three quarters tend to follow the contours of the outer surface; the upper portion becoming infilled to form a shallow central groove which is flanked by another groove on each side.

Scutum (Pl. 1, figs 19, 20) trapezoidal in outline and the width is about three-quarters of the length. The apex is acute and bowed towards the tergum. The apico-basal ridge is moderately to strongly developed; it is rounded at the apex, but rapidly splays out and becomes almost flattened at the base. A second, sharper ridge extends from the apex to the basal margin and is displaced a little towards the occludent side of the midline. Between these two ridges the valve is almost flat;

it is rounded on the occludent side and flatly depressed on the tergal side. Longitudinally it is almost flat, or distinctly concave toward the apex. The basi-lateral angle is narrowly rounded. The basal margin is almost straight. The rostral angle, which is sharp in young valves, becomes very slightly produced as growth advances. The occludent margin is regularly convex. The tergal margin is short, thickened and slightly concave. The tergo-lateral angle is sharp and the tergal margin is inclined with the lateral margin at about 120°. The lateral margin is longer than the tergal margin and slightly concave. The growth lines are not prominent. The surface ornament consists of numerous longitudinal ridges, which are generally stronger on the occludent side of the second ridge. On the inner surface a small pit overlaps the adductor muscle pit and a thin ridge extends a little way down from the apex on each side.

Tergum (Pl. 1, fig. 18; pl. 2, figs 2–4) thin and rhomboidal in outline. A curved apico-basal ridge, sharp on the carinal side, is situated about two thirds of the width of the valve towards the carinal margin. The valve is widely and flatly raised along the occludent margin which is bordered by a narrow depression followed by a ridge bordered by another depression. The occludent margin and the shorter upper carinal margin are generally almost straight; the lower carinal margin is straight or slightly sinuous, longer than the upper carinal margin and about the same length as the scutal margin, which is slightly produced where the apico-scutal fold reaches the edge, it is concave in its upper half and somewhat convex in its lower half. In some instances the scutal margin and the apico-basal ridge is produced a little beyond the lower carina margin. Both the carinal angle and that formed by the occludent and scutal margins are sharp. The outer surface is ornamented with obscure longitudinal ridges. The inner occludent and upper carinal edges are narrowly marked with growth lines which form a slightly overlapping fold and the inner upper carinal edge has a peculiar narrow and deep median depression.

Upper latus (Pl. 1, fig. 21; Pl. 2, figs 10, 11) is triangular in outline with the sides almost equal in length. The tergal margin is slightly concave and bounded by a strong, flattened ridge which is slightly grooved along the midline. From this ridge the valve is flat, becoming slightly turned inwards at the basi-scutal angle. The scutal margin is slightly convex and the basal margin is almost straight. A juvenile valve (Pl. 2, fig. 11) is ornamented with strong apico-basal ridges, but in the larger valves they have become almost obsolete.

Sub-carina (Pl. 1, fig. 22; Pl. 2, fig. 1) the width a little more than half the length; it is slightly bowed inwards. The lateral margins are straight; the basal angle is very wide (c. 120°) and the basal margins are excavated. A short spur is produced at the basi-lateral angle. The median ridge is sharp; there is no rounded prominence as seen on the carina and the portions on either side are regularly concave to the lateral margins which are slightly thickened, but not produced to form parietes. The growth lines are a little more prominent than the ornament of longitudinal ridges. On the inner surface a little more than half the length of the valve is marked with growth lines.

Carinal latus (Pl. 2, figs 5, 6) sub-oblong in outline; the height is about two thirds of the length. It may be longitudinally and transversely slightly bowed inward, or longitudinally concave. The apico-basal ridge is curved, strong and barely produced at the basi-inframedian latus angle. The upper margin is concave and the carinal margin is convex; both are bounded by a very thin groove. The basal margin is straight or slightly convex. The inframedian latus margin, which is straight, is shorter than the carinal margin and inclined to the basal margin at an angle of about 117°.

Sub-carinal latus (Pl. 2, fig. 8) sub-triangular in outline and about as wide as high. Transversely it is convex and longitudinally concave. The apex is acute and directed towards the inframedian latus. The carinal margin is convex and about the same length as the concave upper margin; both these margins have rounded edges. A strong ridge passes from the apex to the basi-inframedian latus angle which is slightly produced. The basal margin is slightly convex. The straight inframedian latus margin is half the length of the basal margin and inclined to it at about 130°.

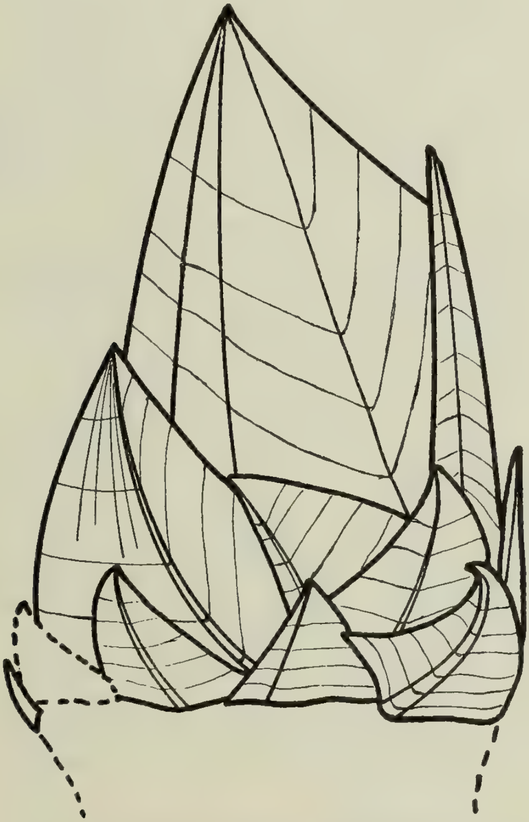

FIG. 1. Reconstruction of *Cretiscalpellum vallum* sp. nov. with the presumed shape of the rostrum in dotted line.

The principal differences between this valve and the carinal latus are in the proportions of the length to width and the less steeply inclined inframedian latus margin.

Subrostrum? (Pl. 2, fig. 12); a unique valve almost triangular in outline with a rounded apex, straight sides and chamfered, broadly curved basal margin; longitudinally and transversely it is very slightly arched and there is a weakly developed median apico-basal ridge, with exceedingly fine striae either side. The growth lines are broken by a series of deeper grooves forming a pattern of elongated hexagonal figures. On the underside two thin ridges either side of the apex extend down to a broad depressed area which follows the lateral edges.

In the absence, in the present collection, of valves corresponding to typical *Cretiscalpellum* rostra, the precise position of this valve remains doubtful. It is comparable however, with valves of similar shape belonging to *C. unguis* (J. de C. Sowerby) from the Gault, which also have a similar hexagonal ornament and chamfered basal margin. These valves are known, by associated material, to have fitted below the rostrum in much the same position as the subcarina fits below the carina.

Rostral latus (Pl. 2, fig. 7) triangular in outline and convex both longitudinally and transversely. A rounded ridge passes from the apex, which is acute, to the basal margin. The rostral margin is convex. The basal margin is concave between the ridge and the rostral angle and convex from the ridge to the inframedian latus angle. The inframedian latus margin is concave.

Inframedian latus (Pl. 2, fig. 9) sub-triangular in outline; on the carinal side a strong ridge extends from the rounded apex to the basal margin and on the carinal side of this ridge the valve is depressed. Longitudinally it is concave. The carinal margin is slightly concave and produced at the basi-carinal angle. The basal and rostral margins are convex.

Discussion: The carina of this species is quite unlike that of any other known *Cretiscalpellum*. The flattened tectum and narrow parietes superficially resembles the illustration of *Arcoscalpellum simplex* (Darwin, 1851, p. 39, pl. 1, figs 9*a–c*), but in *C. vallum* the parietes are set vertically to the lateral margin and not turned inward; also, in *C. vallum* the parietes extend to the basal margin. The tergum, like that of many other species, shows some variation in outline; forms range from rhomboidal with straight margins and an almost straight apico-basal ridge, to trapezoidal with both margins and apico-basal ridge slightly curved.

Three of the carinae, a scutum and a tergum examined, have on the outer surface the remains of a small unidentified bivalve (Pl. 1, fig. 16; Pl. 2, fig. 3). In every case distortion of the valve occurred to accommodate the growth of the mollusc, indicating that the barnacle played the part of 'host' whilst still alive.

The specific name alludes to the walled nature of the parietes of the carina.

Genus ***ARCOSCALPELLUM*** Hoek, 1907

1907 *Arcoscalpellum* Hoek; 1 (31*a*), 59.
1953 *Arcoscalpellum* Hoek; Withers, 3, 199.

Diagnosis: Scalpellidae with the rostral latus low and wide, twice as wide as high, with sub-parallel basal and scutal margins: inframedian latus generally smaller than the other latera, triangular, hour-glass shape or irregular; rostrum comparatively large in the fossil forms, but small or wanting in the Recent forms; carina with the umbo invariably apical; valves in some fossil forms 15, and in Recent forms 14 or 13 in number.

Type species: *A. michelottianum* (Seguenza) = *A. velutinum* (Hoek).

Range: Aptian (Lower Greensand) to Recent.

Arcoscalpellum hubrichti sp. nov.

(Plate 2, Figs 13–20; Plate 3, Figs 1–9; Text-fig. 2)

Diagnosis: Carina moderately to strongly arched transversely and a weakly developed apico-basal ridge. Ridges separate the tectum from the parietes and the parietes from the intraparietes; intraparietes comparatively wide and extending to base of parietes; the base forms almost a right angle, apex open; tectum and parietes ornamented with fine ridges, intraparietes furrowed; growth lines prominent.

Holotype: A carina. 6072PRI. (Pl. 2, figs 13*a–c*), Upper Senonian, Mooreville Chalk; 1½ miles N. of West Greene, Greene County, Alabama.

Material: 485 valves:

British Museum

In.64436–7.	2 Scuta.	Paratypes.	Pl. 2, figs 16*a–b*, 17.	A7
In.64438.	Carina.		Pl. 2, figs 14*a–b*.	A6
In.64439.	Tergum.		Pl. 3, fig. 3.	A1
In.64440–2.	3 Carinal latera.	Paratypes.	Pl. 3, figs 6, 8*a–b*, 9.	A7
In.64443–4.	2 Upper latera.	,,	Pl. 3, figs 4, 5.	A7
In.64445.	Upper latus.	Paratype.		A7
In.64491–2.	2 Carinae.			A1
In. 64493–4.	2 Terga.			A6

Paleontological Research Institution

6072PRI.	Carina	Holotype.	Pl. 2, figs 13*a–c*.	A1
6073*a–b*PRI.	2 Carinae.	Paratypes.	Pl. 2, figs 20*a–b*, Pl. 3, fig. 7.	A1
6074PRI.	Tergum.	Paratype.	Pl. 3, fig. 1.	A1
6082PRI.	25 Carinae & 7 terga.	Paratypes.		A1

Mississippi State University

1323.	Carina.			A1
1324.	Tergum.		Pl. 3, fig. 2.	A3
1325.	Scutum.	Paratype.	Pl. 2, fig. 18.	A7
1356–7.	2 Scuta.	Paratypes.		A7

1358.	Associated carina & tergum.		Pl. 2, fig. 15.	A7
1359.	Upper latus.	Paratype.	Pl. 2, fig. 19.	A3
1360–62.	3 Upper latera.	Paratypes.		A7
1363–65.	3 Carinal latera.	,,		A7
	221 Carinae.			
	34 Scuta.			
	127 Terga.			
	3 Upper latera.			
	36 Carinal latera.			

LOCALITIES: Type-locality, Approx. S.W. corner SE¼ of NE¼ Sec. 27, T.23 N., R.1 W., on public road (through W.M. Steele land), 1½ miles N. of West Greene, Greene County, Alabama. Other localities—A2; A3; A4; A5; A6; A7; A8; A9; A11; M12.

HORIZON: Mooreville Chalk, Upper Senonian.

DESCRIPTION: *Carina* (Pl. 2, figs 13, 14, 20; Pl. 3, fig. 7) robust, moderately to strongly bowed inwards and widening comparatively rapidly from the apex. The width of the tectum is about one fifth the length of the valve; transversely it is moderately to strongly arched, with a weakly developed apico-basal ridge which tends to become obsolete towards the base as growth advances. Stronger, rounded ridges, each composed of two or three parallel minor ridges, separate the tectum from the parietes. The parietes are rather wide, being about half the width of the tectum; they are concave and inclined slightly outwards. The intraparietes extend to the base of the parietes from which they are separated by a prominent rounded ridge; they are inclined almost at right angles to the tectum and are concave, particularly towards the base. At their widest point they are a little more than twice the width of the parietes. The parietes and intraparietes together measure more than half the greatest width of the tectum. The side of the valve measured from the median ridge to the inner edge is deep, varying from about 60 % of the width in young valves, to about 75 % as growth advances. On reaching the basal margin the tecto-parietal and stronger parietal-intraparietal ridges frequently produce prominent knobbly spurs. The inner margin is thick and somewhat sinuous. The outer surface of the tectum and parietes is ornamented with exceedingly fine ridges. Equally fine longitudinal furrows intercept the growth lines on the intraparietes. The growth lines are prominent and slightly ridged. The basal margin forms an angle of about 90°. On the inner surface the valve is open for almost its entire length indicating that only a little of the beak-like apex projected freely.

Scutum (Pl. 2, figs 16–18) thin and trapezoidal in outline; the width being about two thirds of the length. The apico-basal ridge is weakly developed and flatly rounded. Transversely it is flat from the apico-basal ridge to near the occludent margin where it becomes convex; it is flatly depressed on the tergal side. The apex is acute. The occludent margin which is evenly convex, is slightly thickened and bounded by a shallow trough. The rostral angle is sharp and somewhat attenuated.

The basal margin is concave. The basi-lateral angle is bluntly rounded and sometimes slightly produced; the lateral margin is boldly sinuous. The tergal margin, which is straight and shorter than the lateral margin, is deflected into a thin ridge bounded behind by a shallow, tapering furrow.

The surface ornament consists of numerous fine longitudinal ridges which are stronger on the tergal side of the apico-basal ridge. The adductor muscle pit is moderately developed; above, on the occludent side is a slim pit, divided by a faint, sinuous ridge, and bounded by a stronger ridge on the tergal side.

Tergum (Pl. 3, figs 1–3) is elongated and sub-lanceolate in outline. The length ranges from about two and a quarter to two and a half times the width. The apical portion is slender and bowed away from the scutum. A fine apico-basal furrow divides the valve almost along its midline. It is bounded on the scutal side by a low,

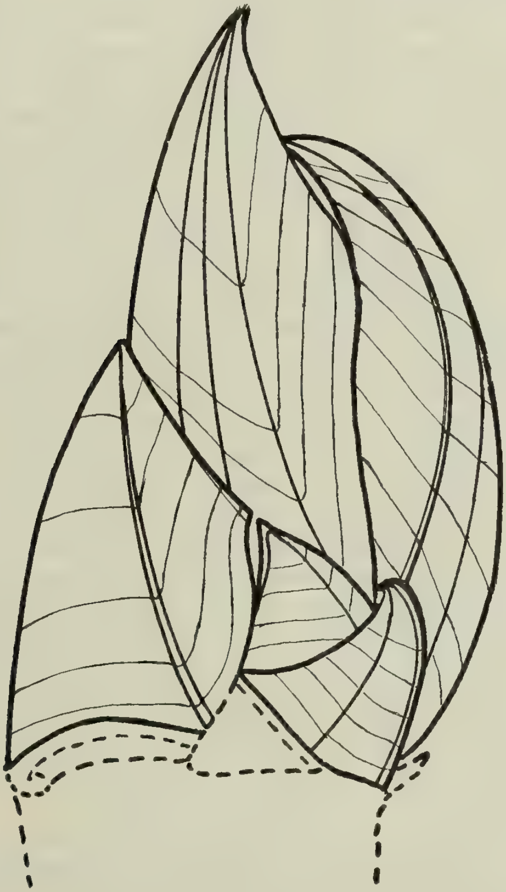

FIG. 2. Reconstruction of *Arcoscalpellum hubrichti* sp. nov. with the presumed shapes of the rostral and inframedian latera and subcarina in dotted lines.

broadly rounded ridge, and a depression separates this ridge from a thickened area bordering the occludent margin. A fine rounded ridge, more noticeable in the smaller valves, extends along the depression from the apex to the scutal margin. The carinal side of the valve is thin and flat. The occludent margin is evenly rounded and equal in length to the scutal margin which may be either rounded or slightly hollowed.

The occludent/scutal angle is obtusely rounded. The carinal margin is distinctly divided into two portions; the upper is concave and the lower, longer portion may be either straight or slightly convex. The carinal angle is broadly rounded. The surface ornament consists of a series of very weak furrows radiating from the apex. The growth lines are fairly coarse and form an acute angle at the midline. The inner occludent and carinal edges are very narrow and marked with growth lines which tend to overlap and produce a slight fold. Very weakly developed longitudinal ridges extend a short distance from the apex. A broad, tapering depression on the occludent side of the midline extends to the scutal margin.

Upper latus (Pl. 2, fig. 19; Pl. 3, figs 4, 5) sub-triangular in outline with the basi-tergal angle broadly rounded. It is transversely and longitudinally slightly convex. A depression, widening towards the base borders the convex tergal margin, which is raised into a slight slip. A ridge bounded by a groove and sometimes a second ridge borders the broadly concave scutal margin. A ledge formed round the tergal and scutal margins becomes thickened and produced beyond the umbo as growth advances. Some variation appears in these ledges in valves of similar size; they may be turned more or less at right angles to the margin, or turned under on the tergal side and deflected widely outward on the scutal side. The basal margin is broadly convex. The growth lines are prominent and, at intervals, widely spaced; they interrupt a few fine longitudinal ridges, which are rather more numerous on the median portion of the valve.

Carinal latus (Pl. 3, figs 6, 8, 9) sub-triangular in outline and transversely and longitudinally convex. The umbo is apical and turned towards the upper latus. A flange developed beneath the upper margin may be directed inwards or deflected obliquely outwards with its apex pointing to the upper latus; this variation occurs in valves of the same growth size. The carinal margin is convex, it is slightly longer than the strongly concave upper margin and generally shorter than the basal margin. The basal margin is weakly convex or nearly straight and sometimes convex on the inframedian side where a rounded ridge extending from the umbo reaches the basal margin. A ridge bounds the carinal margin and the basi-tergal angle is slightly produced; the growth lines on the carinal side of this ridge are upturned. An equally strong ridge bounds the upper margin. The growth lines are rather coarse and fine ridges curve from the apex to the basal margin.

DISCUSSION: The carina of *A. hubrichti* differs from that of *A. withersi* in being wider in relation to its length; by having longer intraparietes; and in becoming splayed out towards the base. The tergum and scutum of *A. hubrichti* are much less robust and, in the tergum the apico-basal fold is central.

A. hubrichti has affinities with *A. fossula* (Darwin), but the carina differs from that of *A. fossula* in having weaker ridges separating the tectum from the parietes, which are less sharply inclined to the tectum and are partly visible when viewed from above. In this respect the carina of *A. hubrichti* resembles that of *A. maximum sulcatum* (J. de C. Sowerby), but an examination of the cross section shows the walls (comprising the parietes and intraparietes) of the latter species generally to be inclined away from the median ridge which is distinctly arched, whereas comparison with the cross section of *A. fossula* (Darwin, 1851, Pl. 1, fig. 4*h*) shows that the walls of both *A. fossula* and *A. hubrichti* (Pl. 3, fig. 10) extend almost parallel from the slightly arched tectum. The sections of carinae of *A. m. sulcatum* figured by Withers (1935, pl. 32, figs 5*c* & 8*b*) are somewhat misleading, since they are taken *below* the maximum development of the intraparietes. The terga of *A. hubrichti* agree very closely with those of *A. fossula*, but differ from those of *A. maximum* (J. de C. Sowerby)—no terga are known of the subspecies *sulcatum*—in maintaining distinct upper and lower carinal margins as growth advances, with no tendency towards developing the crescent shaped appearance of larger specimens of *A. maximum*.

The species is named after Mr Leslie Hubricht, of Meridian, Mississippi, who collected the original material in 1962 and donated it to the Palaeontological Research Institution, Ithaca, New York.

Arcoscalpellum bakeri sp. nov.

(Plate 3, Figs 10–13)

Diagnosis: Carina moderately to strongly bowed inwards; the tectum rounded, with an obscure median ridge; parietes flattened and not easily distinguished from the tectum; intraparietes narrow and inturned except apically where they are produced into a strong ridge.

Holotype: A carina. BMNH In.64446 (Pl. 3, figs 10*a–c*), Maastrichtian, Ripley Formation; Barr Pasture, Oktibbeha County, Mississippi.

Material: 61 valves:

British Museum				
In.64446.	Carina.	Holotype.	Pl. 3, figs 10*a–c*.	M4
In.64447.	Carina.	Paratype.	Pl. 3, figs 11*a–b*.	M3
In.64448.	Carina.	,,	Pl. 3, figs 12*a–b*.	M4
In.64496.	Carina.	,,		OC.7
In.64449.	Tergum.	,,	Pl. 3, fig. 13.	M2
Mississippi State University				
1326.	Carina.	Paratype.		M3
	56 Carinae.			

Localities: Type locality, Barr Pasture, N.W. corner of NE¼ of NW¼ Sec. 6, T.18 N., R.15 E., Oktibbeha County, Mississippi. Other localities—OC.1; OC.2; M2; M3; M5; M9.

Horizon: Middle Ripley, Maastrichtian.

DESCRIPTION: *Carina* (Pl. 3, figs 10*a–c*, 11*a–b*, 12*a–b*) robust and moderately to strongly bowed inward. The length is about four times the width, becoming rapidly splayed out towards the base. The basal margins are slightly rounded and form almost a right angle. Transversely, it is strongly rounded apically, becoming less so towards the base, with a weakly developed apico-basal ridge which sometimes becomes obsolete as growth advances. The parietes are narrow, less than half the width of the tectum, with which they are almost confluent, and much flattened; an obscure ridge separating the tectum from the parietes may be discerned in unworn individuals. The intraparietes are very narrow and almost as long as the parietes, from which they are inclined inward at about 90°, leaving a sharp dividing ridge. As growth advances the apical portions become inflected at a less acute angle and the sides coalesce to form a strongly projecting ridge which usually extends to one third and sometimes a half the length of the valve from the apex. The growth lines are generally not prominent on the tectum and parietes, on the intraparietes they are sharply upturned. The tectum and parietes are ornamented with fine, close set ridges.

A young specimen (In. 64447), 9 mm in length, shows that while the apical portion of the intraparietes is thickened to an extent proportional with larger specimens, the degree of inflexion is slight and the valve is open almost to the apex.

Tergum (Pl. 3, fig. 13) sub-rhomboidal in outline and about twice as long as wide. An obscure, bluntly rounded, almost straight apico-basal ridge is situated more than one third of the width of the valve from the carinal margin. On either side of the ridge the valve is flatly depressed, being steeper on the carinal side. The apex on the only known specimen has been abraded, but was probably bluntly rounded. A slight, raised slip bounds the occludent margin which is moderately convex. The scutal margin is longer than the occludent and is slightly concave in its upper half and convex in its lower half. The upper carinal margin is convex and about half the length of the nearly straight lower portion. The carinal angle is moderately sharp. A very faint groove extends from the apex to near the base of the scutal margin and between this and the apico-basal ridge extend several fine ridges.

DISCUSSION: The carina may be readily distinguished from that of the other species of *Arcoscalpellum* here described by the inflected intraparietes and the infilled, strongly ridged apical portion. These valves show some similarity to Darwin's *S. maximum* var. *cylindraceum* (= *A. maximum solidulum* Steenstrup), figured in Withers, 1935, (Pl. 33, figs 1*a–c*) from the Upper Senonian, *B. mucronata* Zone of Norwich, but differ in the bolder development of the apical ridge and the total infilling of the median cleft at the apex, except in quite juvenile specimens. They differ completely from the massively developed forms of *A. m. solidulum* from the *B. mucronata* Zone of Rügen in which, again, no ridge is present.

This species is named after Mr R. Baker, formerly of the Department of Palaeontology at the British Museum (Natural History), whose constant helpfulness did much to encourage me in my studies.

Arcoscalpellum campus sp. nov.

(Plate 3, Figs 14–16; Plate 4, Figs 1–4)

DIAGNOSIS: Carina very narrow; tectum flattened; parietes narrow; intraparietes set inward from parietes and reaching their greatest width one fourth the distance from the apex.

HOLOTYPE: A carina. BMNH In.64452. (Pl. 3, figs 14*a–b*, Pl. 4, fig. 4) Maastrichtian, Ripley Formation, Bardwell Pasture, Oktibbeha County, Mississippi.

MATERIAL: 59 valves:

BRITISH MUSEUM

In.64450.	Scutum.	Paratype.	Pl. 4, fig. 1.	M5
In.64451.	Tergum.	,,	Pl. 4, figs 2*a–b*.	M5
In.64452.	Carina.	Holotype.	Pl. 3, figs 14*a–b*; Pl. 4, fig. 4.	M5
In.64453.	Carinal latus.	Paratype.	Pl. 3, figs 16*a–b*.	M4
In.64489.	Scutum.	,,		M5
In.64490.	Tergum.	,,		M3

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1327.	Carina.	Paratype.		M3
1328.	Scutum.	,,	Pl. 3, figs 15*a–b*.	M5
1329.	Tergum.	,,	Pl. 4, fig. 3.	M4
1366–73, 1429.	9 Carinae.	Paratypes.		
1374–94.	21 Scuta.	,,		
1395–1414.	20 Terga.	,,		

LOCALITIES: Type locality, Bardwell Pasture, S.W. corner of NE$\frac{1}{4}$ of SW$\frac{1}{4}$ Sec. 6, T.18 N., R.15 E., Oktibbeha County, Mississippi. Other localities—OC.1; OC.2; OC.7; M1; M3; M6; M8; M9.

HORIZON: Ripley Formation, Maastrichtian.

DESCRIPTION: *Carina* (Pl. 3, fig. 14; Pl. 4, fig. 4) moderately bowed inwards and very narrow; the width being from one sixth to one fifth of the length. The basal angle is about 70° and the margins are straight. The tectum is much flattened and gently convex; an almost obsolete apico-basal ridge, which is not raised above the general surface, is delineated by faint grooves. The tectum is separated from the parietes by low, rounded ridges; the parietes are slightly concave and less than half the width of the tectum, with which they are set almost at right angles. The intraparietes are set a little inward from the parietes and are separated from them by a weak ridge; they are almost as long as the parietes, but reach their greatest width at the apical fourth of the length of the valve, where they are as wide as the tectum measured immediately above. Exceedingly fine ridges ornament the tectum and a few occur on the parietes. The inner margin is regularly concave and is open for almost its entire length.

Scutum (Pl. 3, fig. 15; Pl. 4, fig. 1) is thin, trapezoidal in outline and twice as long as wide. Transversely it is moderately convex, being much steeper on the occludent side. Longitudinally, there is a slight median concavity which produces a 'saddle backed' effect; when laid on a flat surface the valve rocks between the tergo-lateral and rostral angles. The apex is acute. The apico-basal ridge is very slight, hardly at all raised and rounded. The basal margin is concave and at right angles to the lateral margin. The occludent margin is very slightly thickened, evenly concave and inclined towards the tergal side. The tergal margin is nearly straight. The tergo-lateral angle is sharp and barely produced, it is inclined with the lateral margin at about 130°. The lateral margin almost equals the tergal margin in length and may be slightly convex or concave. The outer surface is almost smooth; a few longitudinal ridges are generally more prominent on the tergal side. On the inner surface a broad triangular depression, bisected by a thin ridge on the tergal side, extends above the adductor muscle pit to the apex.

Tergum (Plate 4, figs 2–3) thin and sub-triangular in outline; the length slightly exceeds twice the width. A narrow apico-basal fold is situated close to the carinal margin and bowed slightly towards the scutal side. A thin ridge extends from the apex to the scutal margin, bisecting the edge a little to the occludent side of halfway. The valve is slightly depressed on the occludent side of the apico-basal fold, longitudinally it is almost flat. The occludent margin is broadly convex and about the same length as the scutal margin which is slightly concave or sinuous. The scutal angle is obtusely rounded. The carinal margin is generally nearly straight, but sometimes slightly concave in its upper half and broadly convex in its lower half. The surface may be smooth or ornamented with exceedingly fine longitudinal ridges. On the inner surface a thin ridge extends along the occludent side and upper part of the carinal side. A broad ridge, corresponding to the area between the scutal ridge and the occludent margin on the outer surface, extends parallel with the occludent edge. A few growth-lines line the apex, forming a slight overhang, and on some valves hair-like muscle attachment ridges extend a short distance from the apex.

Carinal latus (Pl. 3, fig. 6) triangular in outline. The umbo is acute and turned towards the upper latus, as is the apex of a flange projecting inward below the umbo. The upper margin is moderately concave and shorter than the carinal margin. The carinal margin is strongly convex; the edge is rounded and inflected sharply inwards, the inflected part is bisected longitudinally by a groove. The basal margin is straight for a very short distance on the carinal side, concave in the lower part of the inframedian latus side and upturned toward the upper margin. A comparatively wide part of the valve on the carinal side is raised to form a flat ridge; another, rounded ridge bounds the upper margin and between these ridges the valve is flat. Longitudinally it is flat.

DISCUSSION: The carina may be distinguished from *A. withersi* and *A. hubrichti* by its narrow width, the flatness of the tectum and narrow, inset intraparietes. The 'saddle-backed' section and low apico-basal ridge distinguishes the scutum, while the tergum differs in its lighter build from *A. withersi*, and from *A. hubrichti* in the proximity of the apico-basal fold to the carinal margin.

Among European forms *A. campus* closely resembles *A. comptum* (Withers), of the Group of *A. fossula* (Darwin) from the Aptian and Albian, Gault (Collins, 1965) of S.E. England, but the carina of *A. comptum* is rather more arched transversely and the intraparietes are inflected inwards. The tergum agrees very well in general outline, but the surface ornament is much weaker in *A. campus*, although the portion between the apico-basal fold and scutal ridge is almost plain in both species. The more noticeable difference occurs on the underside, however, where in *A. comptum* the apical growth lines are stronger and several distinct muscle attachment ridges extend from the apex.

The specific name *campus* has a threefold application; it alludes to the flattened tectum of the carina and may be referred to the Bardwell Pasture (type) locality, which is near to the Mississippi State University Campus.

Arcoscalpellum withersi sp. nov.

(Plate 3, Figs 17, 18; Plate 4, Figs 5–15)

DIAGNOSIS: Carina slightly bowed inward; tectum slightly arched apically, becoming flattened towards the base; parietes and intraparietes well developed in line with one another and inclined almost at right angles to the tectum. Other valves generally robust and much thickened.

HOLOTYPE: A carina. BMNH In.64456 (Pl. 4 figs 6*a–c*), Maastrichtian, Ripley Formation; Barr Pasture, Oktibbeha County, Mississippi.

MATERIAL: 325 valves:

BRITISH MUSEUM

In.64454–5.	2 Rostral latera.	Paratypes.	Pl. 3, figs 17–18.	M5
In.64456.	Carina.	Holotype.	Pl. 4, figs 6*a–c*.	M3
In.64457.	Tergum.	Paratype.	Pl. 4, fig. 11.	M3
In.64458.	Tergum.	,,		M3
In.64459.	Scutum.	,,	Pl. 4, fig. 8.	M4
In.64460.	Scutum.	,,		M3
In.64461.	Carinal latus.	,,	Pl. 4, figs 14*a–b*.	M4
In.64462.	Upper latus.	,,	Pl. 4, fig. 15.	M4
In.64463.	Carina (apical half)	,,	Pl. 4, figs 7*a–b*.	M3
In.64480.	Carina.			OC.7
In.64481.	Tergum.			M6

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1330.	Carina.	Paratype.	Pl. 4, fig. 5.	OC.7
1331.	Scutum.	,,	Pl. 4, figs 9*a–b*.	M3
1426.	Scutum.	,,	Pl. 4, fig. 13.	M4
1332, 1425.	2 Terga.	Paratypes.	Pl. 4, figs 10, 12.	M2
1333, 1424.	2 Rostral latera.	,,		M4
1415.	Carina.	,,		OC.7

Other Material (including many fragmentary valves) 115 carinae; 67 scuta; 125 terga; 10 rostral latera.

Localities: Type locality, Barr Pasture, N.W. corner NE¼ of NW¼ Sec. 6, T.18 N., R.15 E., Oktibbeha County, Mississippi. Other localities—OC.1; OC.2; OC.5; OC.7; M1; M2; M5; M6; M8; M9.

Horizon: Ripley Formation, Maastrichtian.

Description: *Carina* (Pl. 4, figs 5–7) comparatively narrow and slightly bowed inwards; the length is about five times the width. The tectum is narrow and slightly arched apically, with a weakly developed apico-basal ridge which becomes almost flat as growth advances. A sharp ridge separates the tectum from the parietes, which are two thirds the width of the tectum, set almost at right angles to it and slightly splayed outwards. A fine ridge separates the parietes from the intraparietes. The intraparietes are in line with the parietes, thin and fairly short, being half the length of the valve; at their widest they are more than twice the width of the parietes measured immediately above. As growth advances the intraparietes sometimes extend slightly beyond the umbo. In some instances a pronounced rib-like growth line is developed on the intraparietes which, progressing outward from near the apex, may bisect the parietal/intraparietal ridge and continue obliquely across the parietes to the tectum. The basal margin is rectangular and forms an angle of about 74°. The tectum is ornamented with exceedingly fine ridges. The inner surface is deeply concave and open to the apex.

Scutum (Pl. 4, figs 8, 9, 13) trapezoidal in outline and generally robust. The width is from half to almost two thirds of the length according to growth size. The apex is blunt. The apico-basal ridge is bluntly rounded and steep on the tergal side; it is somewhat produced at the basi-lateral angle. Transversely it is flatly depressed on the tergal side and on the occludent side it is flat to near the margin, when it is evenly convex. The basal margin is sinuous and the rostral angle is slightly produced. The occludent margin is nearly straight and set almost at right angles to the base in young valves, but it is bowed toward the tergal side in larger valves; there is a shallow depression parallel to the edge. The tergal margin, which is short and straight, is bounded by a thin ridge. The tergo-lateral angle is barely produced and generally rounded; it is inclined with the lateral margin at about 130°. The lateral margin is generally convex and sometimes excavated at the angles. The surface ornament is composed of numerous, very fine longitudinal ridges. On the inner surface a shallow pit, inclined towards the apex on the occludent side, extends above the deep adductor muscle pit. A very shallow depression lies in the tergo-lateral angle.

Tergum (Pl. 4, figs 10–12) obtusely elongate in outline, rather flat and generally much thickened; the length is about three times the width. The apex is acute and narrowly rounded. A slight apico-basal fold is situated very close to the carinal margin. A slight fold extends from the apex to near the middle of the scutal margin and on the occludent side of this the valve is concave. The carinal margin is not divided into an upper and lower part, but is generally slightly convex at the apex and base, while the median portion is nearly straight. The occludent margin may be straight or slightly concave and is shorter than the scutal margin with which it forms an obtuse angle. The scutal angle is sharply to moderately rounded. The scutal margin is slightly concave in its upper half and convex in its lower half. The outer surface is usually ornamented with fine irregularly spaced longitudinal ridges. On the inner surface a fairly wide part of the carinal and occludent edges is marked with growth lines; both edges are steeply inclined inwards. In some valves the surface is slightly raised in line with the inner occludent edge, and in others there are a few short, fine longitudinal ridges.

Upper latus (Pl. 4, fig. 15) thin and sub-triangular in outline. The apex is slightly inclined towards the scutum, almost flat longitudinally and slightly convex transversely. The umbo is acute; a ledge formed below the tergal margin is inclined inwards and is narrower than that formed round the scutal margin which is inclined obliquely outwards. The tergal margin is slightly convex and somewhat shorter than the scutal margin which is moderately concave. It is bordered by a thin ridge, bounded by a shallow groove which broadens towards the basal angle. The basal margin is boldly convex on the scutal side, becoming almost straight on the carinal side. A faint ridge extends from the apex to the basi-carinal angle; some sharper, finer ridges are more crowded on the carinal side of this ridge than on the scutal side.

Carinal latus (Pl. 4, fig. 14) sub-triangular in outline. The umbo is acute and sharply turned toward the upper latus. The apex of the rather broad flange projecting below the umbo is hook-like and directed toward the carina. The upper margin is deeply concave and shorter than the carinal margin. The carinal margin, which is acutely convex at the apex, becomes almost straight. The edge is rounded and forms a thin ridge on the inner side. The basi-carinal angle is slightly produced and the basal margin is concave on the carinal side and rounded on the shorter inframedian latus side. A ridge runs from the apex to the basi-inframedian latus angle and another bounds the upper margin; several weaker ridges ornament the valve on the carinal side. The valve is convex on the carinal side of the apico-basal ridge and steeply compressed on the inframedian side. Longitudinally it is gently convex.

Rostral latus (Pl. 3, figs 17, 18) about twice as wide as high, much thickened and flat transversely. An obscure ridge extends from the apex to the lower part of the inframedian latus margin; on the rostral side of this ridge the valve is excavated and above it another obsolete 'ridge' extends to the middle of the inframedian latus margin; between this and the upper margin the valve is again excavated. The apical angle approaches 90°. The upper margin is slightly concave and bounded by a ridge. The rostral margin is inclined towards the inframedian latus, almost straight and bounded by a thin sharp ridge. The basi-rostral angle is rounded and the basal margin is slightly concave. The inframedian latus margin is slightly concave in its upper half and convex in its lower half.

DISCUSSION: Differences with *A. hubrichti* have been discussed above. The carina differs from that of *A. campus* in that the intraparietes are wider and are in line with the parietes. The species clearly belongs to the Group of *A. fossula*; the carina agrees very closely with the Maastrichtian species *A. gracile* (Bosquet), but differs in being moderately carinated apically and the ridge separating the parietes from the intraparietes (which are inclined a little outwards in *A. gracile*) retains more or less the same thickness towards the base. These ridges are not so strongly developed in *A. withersi* as they are in *A. fossula.*

This species is named after the late Mr T. H. Withers who contributed so largely to our knowledge of fossil cirripedes.

Genus ***Virgiscalpellum*** Withers 1935

1935 *Scalpellum* (*Virgiscalpellum*) Withers, p. 283

1945 *Virgiscalpellum* Withers, (11), 12, p. 554

Diagnosis: carinal umbo sub-apical to sub-central; scutum with umbo sub-central to sub-basal; rostrum much elongated; known valves fourteen.

Type Species: *V. beisseli* (Bosquet & Müller).

Distribution: Lower Aptian ('Crackers', Lower Greensand) to Maastrichtian.

Virgiscalpellum gabbi (Pilsbry)

1926 *Scalpellum* sp. Wade: 191, pl. 62, figs 3, 4, (non figs 6, 7).
1926 *Scalpellum gabbi* Wade (*nom. nud.*) pag. cit.
1931 *Scalpellum gabbi* Wade (*nom nud.*): 20 (Opinion 118).
1933 *Scalpellum gabbi* Pilsbry: 284.
1935 *Scalpellum* (*Virgiscalpellum*) *gabbi* (Pilsbry): Withers: 298, figs 1, 2.
1945 *Virgiscalpellum gabbi* (Pilsbry): Withers: 554.
1953 *Virgiscalpellum gabbi* (Pilsbry); Withers: 16, 18, figs 26, 27.

Diagnosis: Carina angularly bent longitudinally, umbo situated from one fifth to a half the distance from the apex; valve strongly and narrowly convex transversely; inner margin open and concave to infilled; intraparietes marked off from parietes by a strong ridge. Surface ornamented with fine close-set ridges radiating from the umbo, the transverse growth ridges equally raised and prominent.

Virgiscalpellum gabbi gabbi (Pilsbry)

(Plate 4, Figs 16–18; Plate 5, Figs 1–11, 14; Text-fig. 3)

Diagnosis: Umbo of carina reaching to half the distance from the apex, wider above the umbo; markedly constricted laterally immediately below umbo; lower and upper limb of valve open to infilled.

Holotype: A carina (Wade, 1926, pl. 62, figs. 3–4) United States National Museum. No. 73114, Maastrichtian, Ripley Formation, Coon Creek, McNairy County, Tennessee.

Material: 354 Valves:

British Museum

In.64487.	Carina.		Pl. 5, figs 14*a–c*.	OC.1
In.64464.	Carina.		Pl. 4, figs 18*a–b*.	OC.1
In.64465–6.	2 Carinae.		Pl. 5, figs 9*a—b*.	M2
In.64467.	Scutum.	Paratype.	Pl. 5, figs 3*a–b*.	M2
In.64468.	Tergum.			M2

In.64469.	Tergum.		Pl. 5, fig. 4.	OC.2
In.64470.	Scutum.	Paratype.	Pl. 5, fig. 7.	M2
In.64471.	Scutum.	,,		M2
In.64472.	Tergum.		Pl. 5, figs 1*a*–*b*.	M2
In.64473.	Carinal latus.	Paratype.	Pl. 5, fig. 8.	
In.64474.	Upper latus.		Pl. 4, fig. 16.	
In.64475.	Rostral latus.	Paratype.	Pl. 5, fig. 6.	
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1334.	Carina.		Pl. 4, figs 17*a*—*b*.	M8
1416.	Carina.		Pl. 5, figs 10*a*–*b*.	M8
1335.	Tergum.		Pl. 5, fig. 2.	M2
1336.	Scutum.	Paratype.	Pl. 5, fig. 11.	M2
1337.	Rostral latus.	,,	Pl. 5, fig. 5.	M3
	112 Carinae.			
	69 Scuta.			
	154 Terga.			
	1 Rostral latus.			

LOCALITIES (Present collections): OC.1; OC.2; OC.3; M1; M2; M3; M4; M5; M6; M8; M9.

HORIZON: Ripley and basal Prairie Bluff Formations, Maastrichtian.

DESCRIPTION: *Carina* (Pl. 4, figs 17, 18; Pl. 5, figs 10, 14, 18) subject to considerable variation in structure. The position of the umbo varies from central in a specimen measuring about 10 mm in length, to one third the distance from the apex in larger specimens. The angle formed by the upper to the lower limb is between 52°–65°. In some valves the intraparietes are inflected inwards at a very early stage in growth; the inflection occurring immediately below the umbo and producing a waisted appearance (as seen in the figure of the Type; Withers, 1935, pl. 39, fig. 1). Growth may continue with this waist, or as is sometimes the case, the inward development of the intraparietes is continued until they unite at the midline. A thickening of the valve usually ensues along the lower limb, but sometimes the upper limb is affected also. In extreme instances the lower limb is fused solid with the exception of a thin median groove widening distally. Viewed from the side the valve is very slender when advanced infilling occurs early in growth. In other valves the intraparietes are thin, straight and almost parallel; on the inner surface, the valve is open and regularly concave for its entire length.

Scutum (Pl. 5, figs 3, 7, 11) trapezoidal in outline and generally thin, rarely much thickened. The apical part of the valve is much attenuated. The umbo is subcentral and situated a little nearer to the rostral angle; there is a prominent ridge curving slightly upwards and across the valve to the basi-tergal angle. Another strong ridge extends from the umbo to near the rostral angle, and on the rostral side of this ridge the valve is inclined inwards. A slight furrow bordered below by a ridge, extends from the umbo to a short distance from the apex on the tergal margin, and from this furrow to the occludent margin the valve is flat and directed outwards. The occludent margin is almost straight and the upper portion inclined slightly towards the tergal side. The basal portion of the basi-carinal margin is straight and stands almost at right angles to the occludent margin, the rest of the basi-carinal margin is sharply inclined upwards to the basi-tergal angle which is moderately to broadly rounded. The tergal margin is somewhat concave, with a little protuberance near the furrow extending from the umbo; it forms an angle of about 30° with the upper part of the basi-carinal margin. On the outer surface a number of fine ridges radiate from the umbo; they are more prominent in the lower half of the valve and in the region of the umbo. On the inner surface the inner occludent edge is narrow above and below the umbo, but below the umbo it is somewhat excavated. The adductor muscle pit, which is wide and deep, is overhung by a strong, wide ledge which extends upwards from the inner occludent edge and ends abruptly about one third the width of the valve from the tergal edge.

Tergum (Pl. 5, figs 1, 2, 4) obtusely triangular in outline and elongated, being more than two and a half times as long as wide; it is slightly curved towards the carina. An obscure apico-basal ridge, not to be seen in some valves, is situated less than one third the distance from the carinal margin. The occludent and scutal margins are slightly convex and about the same length. The concave carinal margin is only obscurely divided into two parts as the margin is abruptly inturned from the outer surface. The apex and basal angle are narrowly rounded. A prominent rounded ridge extends from the apex near and parallel with the occludent margin; another ridge, more prominent in some valves than in others, extends from the apex to the scutal margin midway between the outer and apico-basal ridges; there are numerous fine longitudinal ridges on the occludent half of the valve. On the inner surface the inner occludent and the inner upper carinal edge are narrow and almost equal in width, and marked with growth lines.

Carinal latus (Pl. 5, fig. 8) wider than high; the upper inner angle is produced upwards to form an acute angle. The carinal margin is very short and convex, it is turned over to produce a rounded edge, which on the inner surface overhangs a little on the carinal side of the umbo. The upper margin is long and concave. The basal margin is concave. The inframedian lateral margin is concave in its upper two thirds and the lower third is produced outwards with a narrowly rounded angle. A raised rounded ridge extends from the umbo to the upper inner angle and from this ridge the upper margin is abruptly inturned. A second ridge extends from the umbo to the inner angle of the basal margin; three much lighter ridges extend from the umbo to the inframedian latus margin.

Rostral latus (Pl. 5, figs 5–6) about twice as wide as high and strongly bowed inwards. A deep fold, ridged on the rostral side, extends obliquely from the apex to the lower part of the inframedian latus margin. The apical angle is acute and rounded. The upper margin is convex and the rostral margin truncated. The basal margin is concave and somewhat longer than the inframedian latus margin which is concave where the fold reaches the edge and convex to the very sharp angle with the upper margin.

The upper latera (Pl. 4, fig. 16) in the present collection add little to our knowledge of the valve, apart from extending the known distribution.

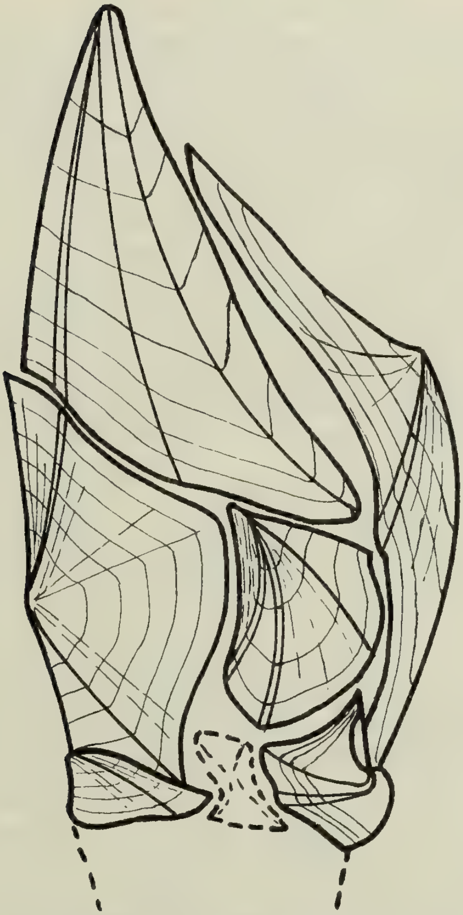

FIG. 3. Reconstruction of *Virgiscalpellum g. gabbi* (Pilsbry) with the presumed shape of the inframedian latus in dotted lines.

DISCUSSION: *V. gabbi* does not appear to have any close affinities with the species described by Pilsbry & Olssen (1951) from South America, but more closely resembles two European Maastrichtian species. The carina resembles that of *V. hagenowianum* (Bosquet), but differs in having the parietes divided from the intraparietes which are narrow and curved (not straight in the lateral view as in *V. hagenowianum*) and generally in being much thickened; whereas in its somewhat attenuated apex, straight occludent margin and general surface ornament, the scutum of *V. gabbi* approximates that of *V. radiatum* (Bosquet). So far, no scutum has been ascribed to *V. hagenowianum* and *V. radiatum* is known only by scuta. The similarities shown by the *V. hagenowianum* carina and *V. radiatum* scuta to corresponding valves of *V. gabbi* support Withers' opinion (1935, p. 297) that the *V. radiatum* scuta should belong to *V. hagenowianum*. With regard to the terga, those of *V. gabbi* appear to differ from *V. hagenowianum* only in having a stronger apico-scutal ridge set further from the occludent margin and a more prominent depression on the occludent side.

Rostral latera for only two species of *Virgiscalpellum* have hitherto been described; those here attributed to *V. gabbi* closely resemble *V. darwinianum* (Bosquet), but differ in having fewer ridges extending to the inframedian latus margin and in the more acute angle formed by that margin with the upper margin.

Virgiscalpellum gabbi apertus sub-sp. nov.

(Plate 5, Fig. 15)

DIAGNOSIS: Carina strongly and broadly convex transversely, umbo reaching one third the distance from the apex, narrower above the umbo; laterally nearly straight; inner surface broadly open throughout its length.

HOLOTYPE: A carina. BMNH In.64478 (Pl. 6, figs 17*a–c*), Maastrichtian, Ripley and basal Prairie Bluff, Catalpa Creek, Oktibbeha County, Mississippi.

MATERIAL: 10 valves:

BRITISH MUSEUM				
In.64478.	Carina.	Holotype.	Pl. 5, figs 15*a–c*.	OC.6
In.64488.	Carina.	Paratype.		M4
MISSISSIPPI STATE UNIVERSITY				
1338.	Carina.	Paratype.		M8
1417–23.	7 carinae.	Paratypes.		

LOCALITIES: Type locality, Catalpa Creek, NW$\frac{1}{4}$ of NE$\frac{1}{4}$ Sec. 25, T.18 N., R.14 E., Oktibbeha County, Mississippi. Other localities—OC.1; M4; M7; M8.

HORIZON: Ripley and basal Prairie Bluff, Maastrichtian.

DESCRIPTION: *Carina* (Pl. 5, figs 15*a–c*) very broad, the basal width being about a quarter of the length. The umbo is sharp and situated from one fifth to one third of the length of the valve from the apex. The apical and basal margins are broadly rounded. The tectum is not differentiated from the parietes; the upper and lower limbs are weakly carinated at the umbo, becoming evenly rounded distally. The upper limb is narrower than the lower, which splays out a little towards the base. The intraparietes are separated from the parietes by a strong ridge and extend almost at right angles with the tectum. The inner margin is more or less divided into two portions, angularly bent just above the parietal ridge; the upper portion comprising the intraparietes, is almost straight and the lower portion is convex. The outer surface is ornamented with fine ridges and the growth lines are rather more prominent on the intraparietes than on the tectum. The inner surface is widely, deeply and regularly concave and open throughout the length of the valve.

DISCUSSION: The carina of *V. g. apertus* may most readily be distinguished from that of *V. g. gabbi* by the broadly open inner surface with little or no indication of the intraparietes turning in to form a waist below the umbo; it is wider in relation to length; the upper limb is comparatively shorter and the intraparietes are wider and usually straighter.

The trivial name refers to the open inner surface of the valve.

Virgiscalpellum sp.

(Plate 5, Fig. 12)

MATERIAL: A unique scutum, BMNH. In.64476.

LOCALITY: 4½ miles S. of West Point, NE¼ of SE¼ Sec. 6, T.19 N., R.16 E., Clay County, Mississippi.

HORIZON: basal Annona or upper Coffee Formation, Campanian, Upper Senonian.

DESCRIPTION: Scutum sub-trapezoidal in outline and bowed outwards. The umbo is sub-central, being situated a little nearer to the base. A wide, indistinct fold extends from the umbo to the basi-tergal angle and above this fold the valve is concave to near the upper part of the occludent margin, which is rather widely raised and bounded below by an indistinct depression. The tergal margin is nearly straight and forms an angle of about 40° with the upper half of the occludent margin. The basal margin is very short, straight and inclined toward the tergum. The upper occludent margin is inclined with the lower occludent margin at an angle of about 67°; both margins are slightly convex. Very fine ridges extend from the umbo within the basi-tergal fold and the occludent depression, but on the central portion of the valve the ridges become so wide and depressed as to be outlined only by faint grooves. On the inner surface a broad, rounded ridge extends parallel to the upper occludent edge and at the umbo it slightly overhangs the comparatively large, almost circular adductor muscle pit.

DISCUSSION: The broadly angled occludent margin and straight tergal margin at once distinguishes this valve from scuta of *V. gabbi*. Indeed the straight tergal margin distinguishes it from any other known *Virgiscalpellum* scutum; it is preferable for additional material to be examined before reaching a more definite taxonomic opinion.

Virgiscalpellum sp.

(Plate 5, Fig. 13)

MATERIAL: A unique tergum, BMNH In.64477.

LOCALITY: ½ mile E. of State College, probably near Centre W½ of NW¼ Sec. 6, T.18 N., R.15 E., Oktibbeha County, Mississippi.

HORIZON: upper Ripley Formation, Maastrichtian.

DESCRIPTION: Tergum sub-triangular in outline and about two and a half times as long as wide; it is flat transversely and longitudinally slightly convex. A rounded apico-basal ridge rises from a shallow fold one fourth the length of the valve from the apex; it is bowed towards the carina both at the apex and base. The apex is bluntly rounded and bowed toward the carina. A strong, curved ridge extends from the apex to high on the scutal margin, and a much weaker ridge extends below this to the lower third of the scutal margin. Both ridges are slightly produced at the margin. The occludent margin is convex and bordered by a slightly raised and rounded slip. The scutal angle is acute and sharp. The scutal margin, which is almost twice the length of the occludent, is nearly straight from the scutal angle to the lower ridge, and convex to the base. The carinal margin is concave in its upper half and convex in its lower half. On the outer surface a few longitudinal ridges occur between the lower occludent and the apico-basal ridges. On the inner surface a very narrow ridge curves across the apex and extends down the lower occludent edge.

Discussion: This valve differs from that of *V. gabbi* in its shorter occludent margin and subsequently longer scutal margin, and in its relatively straighter carinal margin. It appears to have no affinities with known South American or European species. With additional material it may prove to be conspecific with the earlier scutum described above.

Sub-order BRACHYLEPADOMORPHA

BRACHYLEPADIDAE Woodward 1901

Genus ***BRACHYLEPAS*** Woodward 1901

1901 *Brachylepas.* Woodward: 150.

Diagnosis: Brachylepadidae with the carina cylindrical or semi-conical and the shell laterally flattened or radially symmetrical; three or four whorls of imbricating plates, the outer whorl of plates with a median basal notch; basis probably membranous or calcareous.

Type Species: *B. niassanti* (Hebert).

Range: Cretaceous (Turonian to Maastrichtian).

Brachylepas angulosa sp. nov.

(Plate 5, Fig. 16)

Material: A rostrum, Holotype BMNH. In.64479.

Locality: Barr Pasture, N.W. corner of NE¼ of NW¼ Sec. 6, T.18 N., R.15 E, Oktibbeha County, Mississippi.

Horizon: Ripley Formation, Maastrichtian.

Description: Rostrum robust and almost as wide as high. A sharp, straight median ridge deflects the sides to about 67° and produces the effect of a hollow pyramid. The apex and basal angles are bluntly rounded. Six prominent flattened ribs extend from the apex to the base (the median ridge is caused by a dominant rib on the left side) and give the base an undulating edge. Very fine ribs are intercalated apically. The growth lines are thin, rounded and somewhat beaded where they are crossed by the secondary ribs. The inner surface is thickened along the inner margins and the growth lines extend downwards from the apex for nearly half the length of the valve. Beneath this on either side four or five shallow fluted depressions extend to the basal margin.

Discussion: The angular nature of the valve is unique among the known species of *Brachylepas*, which have an almost semicircular basal outline. The number of ribs is fewer than that generally encountered in *B. niassanti* and the cancellated ornament of the latter is barely developed in *B. angulosa*. Little more can be said of its affinities with the Western species until further valves become available.

The trivial name refers to the basal outline of the valve.

PART II. GEOLOGY

By F. F. MELLEN

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STRATIGRAPHY

Hitherto, cirripedes from the 'Selma chalk' have all but been ignored stratigraphically in favour of other more easily recognized macroscopic and abundant microscopic index fossils. It was thought that cirripedes might be of biostratigraphical importance from the taxonomic study of the Mississippi/Alabama collections. The horizons of the various species were tabulated and it was seen that they are apparently naturally grouped with no inter-horizon overlapping.

The cirripedes of the 'Selma chalk' may be summarized as follows:

Ripley Formation—Navarroan (Maastrichtian):

C. harnedi, A. bakeri, A. campus, A. withersi, V. g. gabbi, V. g. apertus, B. angulosa.

Basal Annona—Tayloran (Campanian):

C. vallum.

Middle Mooreville—Austinian (Santonian):

C. macrum, C. venustum, A. hubrichti.

The genus *Virgiscalpellum* is restricted to the Ripley and the basal part of the overlying Prairie Bluff. This is overlain almost directly by deposits which contain *Diploschiza melleni*, a small bivalve used as an index fossil in the Prairie Bluff. Two new species of *Arcoscalpellum* and one of *Cretiscalpellum* found with *Virgiscalpellum* also appear to be restricted to this horizon. The Ripley Formation of Oktibbeha County, Miss., seems to be the most prolific cirripede unit yet described from North America. An attempt has been made to zone this unit on the basis of its cirripede fauna, but other than the one specimen of *B. angulosa*, from the mid-Ripley Barr Pasture Locality (M4) there seems to be no significant variation, apart from an apparent increase in abundance of all forms in the middle and upper parts of this unit.

C. vallum appears to have a restricted vertical range. It is found in deposits of outer neritic sediments at the base of the Annona chalk (which is the equivalent of the upper part of the Coffee Sands) some 20–30 ft below the lowest range of *Diploschiza cretacea*, an important zonal indicator.

A. hubrichti and two new species of *Cretiscalpellum* seem to be restricted to a zone which lies near the mid portion of the 250 ft thick Mooreville chalk (marl).

Approximately 250 ft of chalk, and chalky marl separates the zone containing *Virgiscalpellum* from that with *C. vallum*, while about 200 ft of chalky marl separates the zone containing *C. vallum* with that of *A. hubrichti*.

From these observations it is clear that there are three distinct cirripede biostratigraphic 'zones' within the 'Selma'. These, designated in descending order, are:

Zone of *Virgiscalpellum* (Ripley and basal Prairie Bluff—Maastrichtian).

Zone of *Cretiscalpellum vallum* (basal Annona or upper Coffee—Campanian).

Zone of *Arcoscalpellum hubrichti* (middle Mooreville—Santonian).

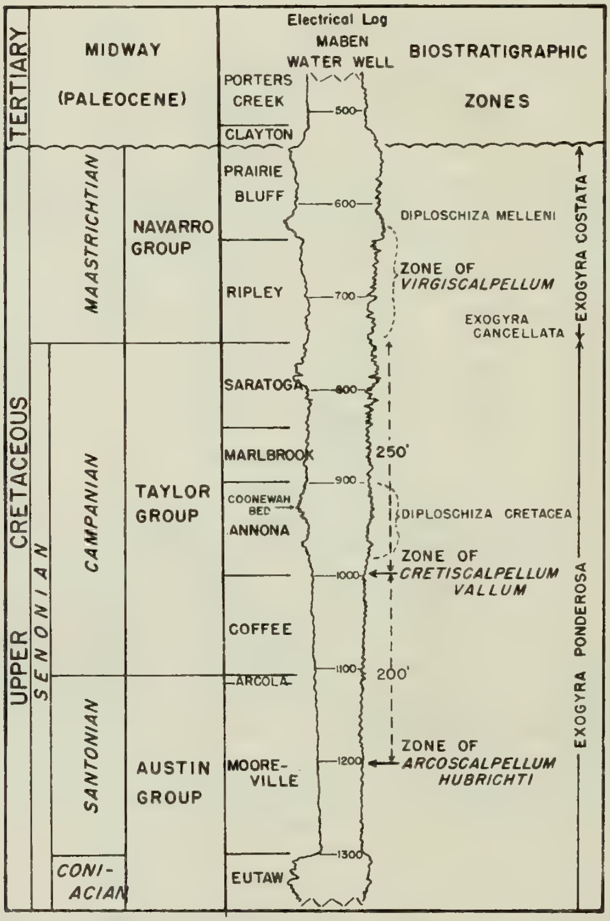
TERTIARY
MIDWAY
(PALEOCENE)
Electrical Log
MABEN
WATER WELL
BIOSTRATIGRAPHIC
ZONES
PORTERS
CREEK
500
CLAYTON
PRAIRIE
BLUFF
600
DIPLOSCHIZA MELLENI
MAASTRICHTIAN
NAVARRO
GROUP
ZONE OF
VIRGISCALPELLUM
RIPLEY
700
EXOGYRA
CANCELLATA
EXOGYRA COSTATA
UPPER CRETACEOUS
SENONIAN
CAMPANIAN
TAYLOR
GROUP
SARATOGA
800
MARLBROOK
250'
900
COONEWAH
BED
ANNONA
DIPLOSCHIZA CRETACEA
ZONE OF
CRETISCALPELLUM
VALLUM
1000
COFFEE
ARCOLA
1100
200'
SANTONIAN
AUSTIN
GROUP
MOORE-
VILLE
1200
ZONE OF
ARCOSCALPELLUM
HUBRICHTI
EXOGYRA PONDEROSA
1300
CONI-
ACIAN
EUTAW

Fig. 4. Correlation and biostratigraphic zones in 'Selma chalk' represented on a selected electrical log, Maben Water Well, SE. ¼ of SW. ¼ of NW. ¼ of Section 31, T. 20 N., R. 12 E., Oktibbeha County, Mississippi. Elevation 466 feet. Position of Zone of *Cretiscalpellum vallum* is interpreted at 1000 feet (—534). This Zone crops out at elevation 200 feet on south valley wall of Tibbee Creek, NE. ¼ of SE. ¼ of Sec. 6, T. 19 N., R. 16 E., Clay County, 24½ miles to the east. The westerly dip of 734 feet is at an average rate of 30 feet per mile, slightly less than the rate of 'true' dip, which is west-southwesterly, about 35 feet per mile.

Geographical range: The zone of *Virgiscalpellum* has been established over an outcrop distance of 155 miles from Coon Creek, McNairy County, Tennessee, to south central Noxubee County, Mississippi. Although most, if not all, of the six species recorded appear possibly to be restricted to this zone, the designation is chosen because *V. gabbi* (Pilsbry) was first reported (by Wade) from the lower Ripley Coon Creek beds of Tennessee; also, this species is the dominant one throughout the Ripley of Oktibbeha County, Mississippi.

The zone of *Cretiscalpellum vallum* has been established over an outcrop distance of 56½ miles from Tibbee Creek, Clay County, Miss., to one mile west of Gainesville, Sumter County, Alabama.

The zone of *Arcoscalpellum hubrichti* has been established at many localities in an outcrop belt about two miles wide in Greene County, Alabama; in 1970, Dr E. E. Russell (Mississippi State University) located the species 4 miles west of Columbus, Lowndes County, Miss. (M12), in the Mooreville, in a position estimated to be 50 ft above its base, thus extending the lateral outcrop over a distance of 65 miles between

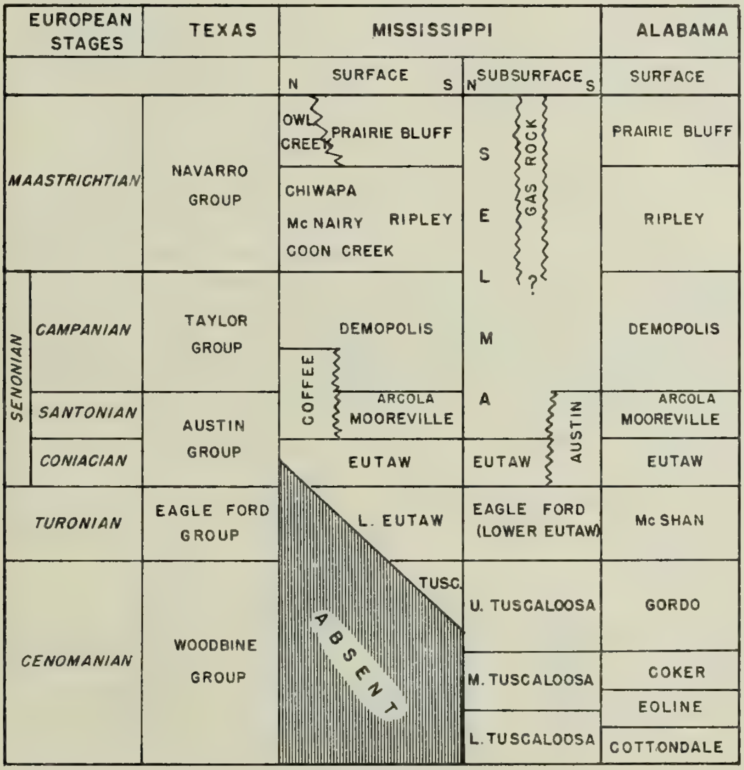
EUROPEAN STAGES
TEXAS
MISSISSIPPI
ALABAMA
N SURFACE S
N SUBSURFACE S
SURFACE
MAASTRICHTIAN
NAVARRO GROUP
OWL CREEK
PRAIRIE BLUFF
CHIWAPA
McNAIRY
RIPLEY
COON CREEK
S E L M A
GAS ROCK
?
PRAIRIE BLUFF
RIPLEY
SENONIAN
CAMPANIAN
TAYLOR GROUP
DEMOPOLIS
COFFEE
DEMOPOLIS
SANTONIAN
AUSTIN GROUP
ARCOLA
MOOREVILLE
AUSTIN
ARCOLA
MOOREVILLE
CONIACIAN
EUTAW
EUTAW
EUTAW
TURONIAN
EAGLE FORD GROUP
L. EUTAW
EAGLE FORD (LOWER EUTAW)
McSHAN
CENOMANIAN
WOODBINE GROUP
TUSC.
ABSENT
U. TUSCALOOSA
GORDO
M. TUSCALOOSA
COKER
EOLINE
L. TUSCALOOSA
COTTONDALE

Fig. 5. Correlation chart showing European stages, Texas Group terminology and Upper Cretaceous stratigraphic nomenclature in Mississippi and Alabama. No attempt was made to show range of hiatuses in Texas or Alabama or in the Mississippi subsurface.

the States. Barnacle valves were also found at Cochrane, Pickens County, Alabama, some 15 miles distant from West Green. Recent search has not re-discovered this particular locality, but as Cochrane is on Mooreville terrain, it is probable that the valves recorded were of *A. hubrichti*. Valves of *A. hubrichti* outnumber those of the accompanying species of *Cretiscalpellum* by a ratio of 200 : 1.

A detailed examination of cores and electrical loggings are needed for greater refinement in the stratigraphical placing of the zones of *C. vallum* and *A. hubrichti*.

Cirripedes of the 'Selma chalk' may well be found in sediments of widely varying bathymetric depths, but the present collection seems to have been preserved best in deposits consisting of thin-shelled molluscs, comminuted shell fragments, fine sands and silts. It is suggested that these deposits were formed on outer neritic bottoms of the continental shelf—in depths of 200–600 ft. A notable exception is *V. gabbi* from highly glauconitic and extremely fossiliferous marls of the basal Ripley, Coon Creek beds of McNairy County, Tennessee, which indicates very shallow marine conditions.

The various formations composing the 'Selma chalk' are tabulated for Alabama, Mississippi and Texas, and correlated with the European Stages (Fig. 5). Below the 'Selma' the lower and upper Eutaw are shallow marine and estuarine sediments and would probably yield a cirripede fauna with intensive collecting. Beneath, the sediments of Tuscaloosa Age are almost entirely continental except in the deepest sub-surface.

CRETACEOUS DEPOSITION

All the present cirripede collections were made from deposits on a platform area lying north of a tectonic hinge which marks the northern limit of the Mississippi Interior Salt Basin. The structure of these deposits indicate a massive step by step transgression of the Mesozoic seas from the south. During the late Upper Cretaceous the area of north Mississippi, west Tennessee, west Kentucky, southeast Missouri and northeast Arkansas was covered by marine water for the first time since the retreat of the shallow Upper Carboniferous (Pennsylvanian) seas, Alleghany Revolution (Rodgers, 1967).

The Appalachian Mountain Chain to the north and northeast and the Nashville-Ozark and Ouachita Uplifts to the north and northwest were probably the provenances of the sediments.

The initial dip (Paleoslope) of the strata of 'Selma' age was in a south easterly direction, except in central Alabama and eastwards, although a period of intense volcanism reached its climax during late Taylor or early Navarro times in west-central Mississippi, southeast Arkansas and northeast Louisiana. This produced the highly uplifted and truncated Jackson Dome and the Sharkey-Monroe Uplift from which sediments and igneous detritus have been eroded. Scattered biotite flakes, pyroclastic granules and pebbles, and bentonite deposits in the shallow water Tuscaloosa, Eutaw, Coffee and Ripley Formations which became increasingly abundant near the volcanic uplifts, would seem to be evidence of the importance of contributions of the late Mesozoic volcanism to the geological history of the area.

It is further suggested that the axis of the Mississippi Embayment and its lateral Desha Basin which extends west into southeast Arkansas were a subsidence caused by the initial uplift of the Jackson Dome and the Sharkey-Monroe Uplift to the west.

LOCALITIES AND COLLECTIONS

Mississippi

'Original Collections'

Cirripede valves, from seven localities and totalling 146, were from the Ripley Formation of Oktibbeha County (140) and from the Tayloran chalk of Clay County (6). Of these, 81 were collected by H. H. Harned, Jr., and 65 by Mellen. At the time these collections were made there were no good maps of the area, consequently the collections were designated:

OC.1. 2 miles E. of State College.
(Probably NW¼ of NW¼, Sec. 5, T. 18 N., R. 15 E., Oktibbeha County.)
OC.2. ¾ mile E. of State College (H.H.H., Jr.)
(Probably Bardwell Pasture, S.W. corner NE¼ of NW¼, Sec. 6, T. 18 N., R. 15 E., Oktibbeha County.)
OC.3. ½ mile E. of State College.
(Probably near Centre W½ of NW¼ Sec. 6, T. 18 N., R. 15 E., Oktibbeha County.)
OC.4. Catalpa Creek.
(NW¼ of NE¼ of Sec. 25, T. 18 N., R. 14 E., Oktibbeha County: basal Prairie Bluff.)
OC.5. 5 miles NW. of State College (Stoney Point).
(SW¼ of SW¼ of Sec. 16, T. 19 N., R. 14 E., Oktibbeha County: basal Prairie Bluff and Upper Ripley.)
OC.6. Tibbee Creek (4½ miles S. of West Point).
(NE¼ of SE¼, Sec. 6, T. 19 N., R. 16 E., Clay County: basal Annona or upper Coffee.)
OC.7. 1½ miles E. of State College—Barr Pasture (H.H.H. Jr.)
(Probably N.W. corner of NE¼ of NW¼ of Sec. 6, T. 18 N., R. 15 E., and other outcrops lying to the northwest and northeast.)

Serial numbers have been included to simplify locality recordings in the text.

Other collections made by Harned during the 1930's were included in material sent directly to Collins later, are marked 'Barr and Bardwell Pastures', 'Barr', and 'Sand Creek and Barr'. It would be imprecise to attempt to assign more specific location descriptions to the old collections due to the fact that some of the old chalk gullies have been completely filled and obliterated in recent years.

Mississippi

'Recent Collections'

M1. 'Oktibbeha County, from Dunn Seiler Museum'—exact localities unknown, but all undoubtedly from the Ripley of the MSU campus area.
M2. Barr & Bardwell Pastures: NE¼ of NW¼ Sec. 6, T. 18 N., R. 15 E., Oktibbeha County (H. H. Harned, Jr., Coll.) (middle Ripley).
M3. Barr Pasture: N.W. Corner of NE¼ of NW¼ of Sec. 6, T. 18 N., R. 15 E., Oktibbeha County (H. H. Harned, Jr. Coll.) (middle Ripley).
M4. Barr Pasture: cf. 'M3'. (middle Ripley)
M5. Bardwell Pasture: S.W. Corner of NE¼ of NW¼ of Sec. 6, T. 18 N., R. 15 E., Oktibbeha County (H. H. Harned, Jr. Coll.). These gullies have been filled and completely obliterated. (middle Ripley)

M6. Sand Creek & Barr: Probably SW¼ Sec. 31, T. 19 N., R. 15 E. & N.W. Corner of NE¼ of NW¼ Sec. 6, T. 18 N., R. 15 E. Oktibbeha County (H. H. Harned, Jr. Coll.). (middle & lower Ripley)
M7. 6 Miles N.W. of Starkville (H. H. Harned, Jr. Coll.) Locality indeterminable, but probably upper Ripley.
M8. N. of Evans Hall: NW¼ of NW¼ Sec. 1, T. 18 N., R. 14 E., Oktibbeha County.
M9. Chapel Hill Church locality of S. valley wall Catalpa Creek, 5 miles S. & 1·75 miles E. of Barr Pasture locality, NE¼ of NE¼ Sec. 32, T. 18 N., R. 15 E., Oktibbeha County.
M10. Trim Cane—Josey Creeks confluence; SW¼ of SW¼ Sec. 20, T. 19 N., R. 14 E., Oktibbeha County.
M11. 4½ miles S. of West Point, S. valley wall of Tibbee Creek, E. of U.S. Highway, 45—W.: NE¼ of SE¼ Sec. 6, T. 19 N., R. 16 E., Clay County. (basal Annona or upper Coffee.)
M12. Cuts in Highway 82 bypass, c. 4 miles W. of Columbus, Secs. 26 & 27, T. 19 N., R. 17 E. Lowndes County.

ALABAMA

A1. Approx. S.W. corner SE¼ of NE¼ Sec. 27, T. 23 N., R. 1 W., on public road (through W. M. Steele land), 1½ miles N. of West Greene, Greene County.
A2. c. 1 mile N.E. of 'A1', c. SW¼ of SE¼, Sec. 23, T. 23 N., R. 1 W., Greene County.
A3. c. 1½ miles N.W. of 'A1', near centre NW¼ Sec. 22, T. 23 N., R. 1 W., Greene County.
A4. 2 miles E. of West Greene, 4 miles N. of Clinton, near Centre SW¼ Sec. 36, T. 23 N., R. 1 W., Greene County.
A5. 3 miles E. of West Greene & 3 miles W. of Clinton, c. ¼ miles N.E. of church, c. Centre SW¼ Sec. 31, T. 23 N., R. 1 E. Greene County.
A6. Mt. Olive Church, around the common quarter corner, Secs. 30 & 31, T. 22 N., R. 1 E., Greene County.
A7. 1·2 miles due E. of Mt. Olive Church and in SW¼ of SW¼ Sec. 32, T. 22 N., R. 1 E., Greene County.
A8. 1 mile S.E. of Mt. Olive Church locality; 1½ miles N.E. of Mt. Olive Church, north of Highway, Greene County.
A9. Shallow washes in brushy area W. of paved road 4½ miles S.S.W. of Eutaw in SW¼ of NE¼ of Sec. 20, T. 21, N., R. 2 E., Greene County.
A10. 1 mile W. of Gainesville, NE¼? Sec. 10, T. 21 N., R. 2 W. Sumter County.
A11. 'Bonanza', SW¼ of SW¼, Sec. 32, T. 22 N., R. 1 E., Greene County.

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PLATE 1

Cretiscalpellum macrum sp. nov. Page 354

Upper Senonian, Mooreville Chalk.

FIG. 1. Carina. Outer view. Holotype. In.64414. A5 : Greene County, Alabama.
FIG. 2. Carina. Outer view. A8. Paratype. MSU 1311.
FIG. 3. Scutum (right). Outer view. A1. Paratype. In.64415.
FIG. 4. Tergum (right). Outer view. A4. Paratype. In.64416.
FIG. 5. Tergum (left). Outer view. A8. Paratype. MSU 1312.
FIG. 6. Tergum (left). Outer view. A8. Paratype. In.64417.
FIGS. 1–6 ×2 diam.

Cretiscalpellum venustum sp. nov. Page 356

Lower or middle Mooreville Chalk, Upper Senonian.

FIG. 7. Carina. *a*, outer view; *b*, side view. Holotype. In.64418. A7 : Greene County, Alabama.
FIG. 8. Carina. Outer view. A8. Paratype. MSU 1313.
FIG. 9. Tergum (left). Outer view. A8. Paratype. In.64419.
FIGS. 7–9 ×2 diam.

Cretiscalpellum harnedi sp. nov. Page 357

Maastrichtian, Middle Ripley Formation.

FIG. 10. Scutum (right). *a*, outer view; *b*, inner view. M8 Paratype. In. 64420.
FIG. 11. Carina. *a*, side view; *b*, outer view; *c*, inner view. Holotype. In.64421. M3: Oktibbeha County, Mississippi.
FIG. 12. Tergum (right). *a*, outer view; *b*, inner view. M8. Paratype. In.64422.
FIGS. 10–12 ×4 diam.

Cretiscalpellum venustum sp. nov. Page 356

FIG. 13. Transverse section of carina, MSU 1313 at apex, c. ×8 diam.

Cretiscalpellum vallum sp. nov. Page 358

Upper Senonian, basal Annona or upper Coffee Formation.

FIG. 14. Carina. *a*, outer view; *b*, inner view, ×2 diam. M11. Paratype. MSU 1316.
FIG. 15. Carina. *a*, outer view; *b*, side view, ×2 diam. Holotype. In.64423. M11: Clay County, Mississippi.
FIG. 16. Carina, with small bivalve on the outer surface, ×2 diam. M11. Paratype. MSU 1355.
FIG. 17. Transverse sections of carina, In.64423, at *a*, c. 7·0 mm and *b*, c. 14·0 mm from apex. c. ×5 diam.
FIG. 18. Tergum (right). Outer view, ×2 diam. M11. Paratype. In.64426.
FIG. 19. Scutum (left). Outer view, ×4 diam. M11. Paratype. MSU 1317.
FIG. 20. Scutum (left). *a*, outer view; *b*, inner view, ×2 diam. M11. Paratype. In. 64425.
FIG. 21. Upper latus. Outer view, ×4 diam. M11. Paratype. MSU 1319.
FIG. 22. Subcarina. *a*, inner view; *b*, outer view, ×2 diam. M11. Paratype. In.64424.

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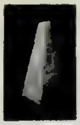
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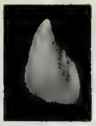
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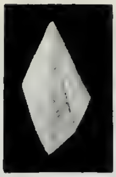
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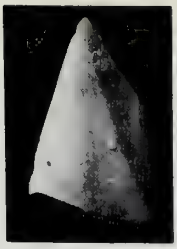
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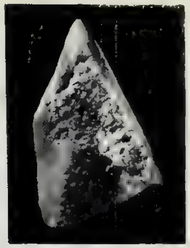
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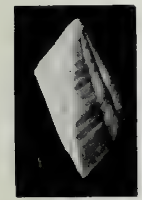
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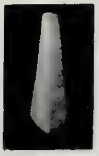
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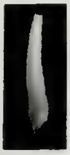
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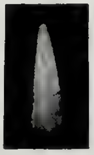
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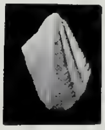
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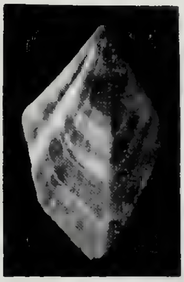
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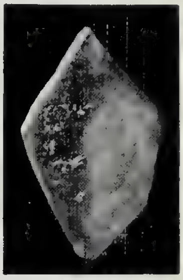
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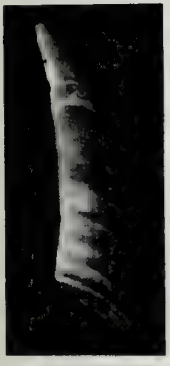
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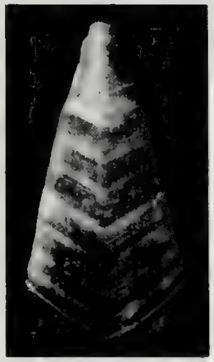
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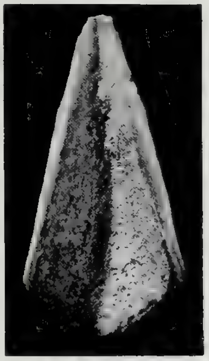
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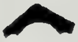
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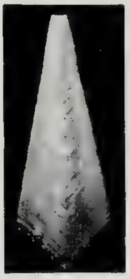
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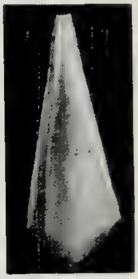
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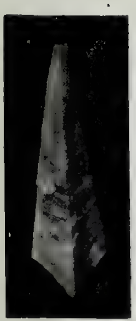
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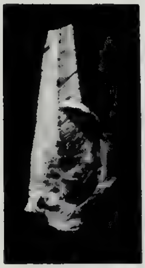
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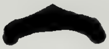
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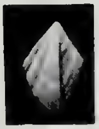
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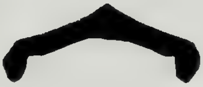
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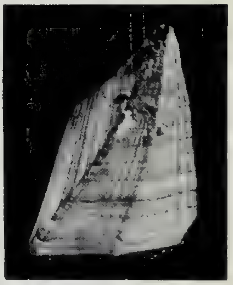
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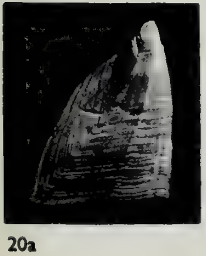
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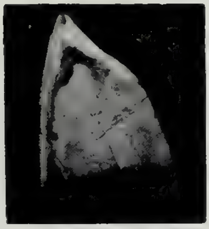
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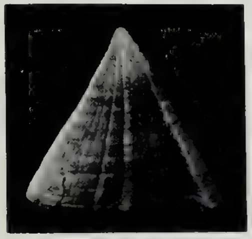
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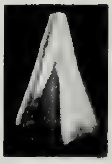
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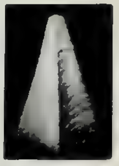
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PLATE 2

Cretiscalpellum vallum sp. nov. Page 358

FIG. 1. Subcarina. Outer view, ×4 diam. M11. Paratype. MSU 1320.

FIG. 2. Tergum (left). *a*, inner view; *b*, outer view, ×2 diam. M11. Paratype. In.64428.

FIG. 3. Tergum (left), with small bivalve on the outer surface, ×2 diam. M11. Paratype. In.64435.

FIG. 4. Tergum (left). Outer view, ×4 diam. M11. Paratype. MSU 1318.

FIGS 5–6. Carinal latera (left & right). Outer views, ×4 diam. M11. Paratypes. In. 64433–34.

FIG. 7. Rostral latus (left). Outer view, ×2 diam. M11. Paratype. In.64429.

FIG. 8. Subcarinal latus (right). Outer view ×4 diam. M11. Paratype. In.64430.

FIG. 9. Inframedian latus. Outer view, ×4 diam. A10. Paratype. In.64431.

FIG. 10. Upper latus. Outer view of juvenile valve, ×6 diam. OC.6. Paratype. In. 64432.

FIG. 11. Upper latus. Outer view, ×4 diam. M11. Paratype. In.64427.

FIG. 12. Subrostrum. Outer view, ×4 diam. M11. Paratype. In.64483.

Arcoscalpellum hubrichti sp. nov. Page 363

Upper Senonian, Mooreville Chalk.

FIG. 13. Carina. *a*, outer view; *b*, side view; *c*, inner view, ×2 diam. A1 : Greene County, Alabama. Holotype. 6072PRI.

FIG. 14. Carina. *a*, outer view; *b*, side view, ×2 diam. A6. In.64438.

FIG. 15. Carina and associated left tergum which has become orientated through 180°. Outer view, natural size. A7. MSU 1358.

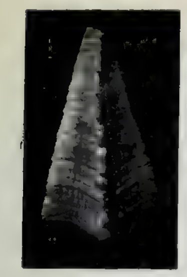
FIG. 16. Scutum (right). *a*, outer view; *b*, inner view, ×2 diam. A7. Paratype. In. 64436.

FIG. 17. Scutum (left). Outer view, ×2 diam. A7. Paratype. In.64437.

FIG. 18. Scutum (left). Outer view, ×2 diam. A7. Paratype. MSU 1325.

FIG. 19. Upper latus (right). Outer view, ×4 diam. A3. Paratype. MSU 1359.

FIG. 20. Transverse sections of carinae; at *a*, 10·0 mm & *b*, 15·0 mm from the apex, c. ×4 diam. Paratypes. 6082*a*–6082*b*PRI.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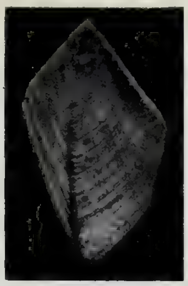
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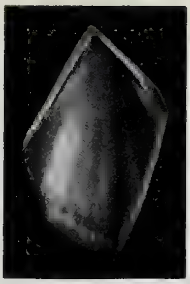
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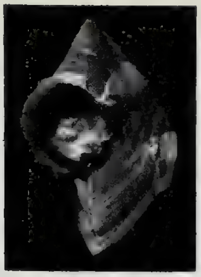
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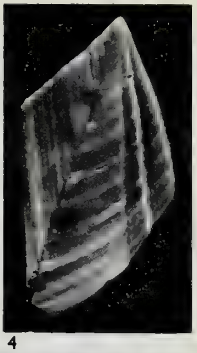
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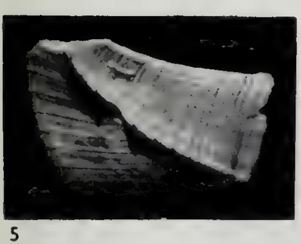
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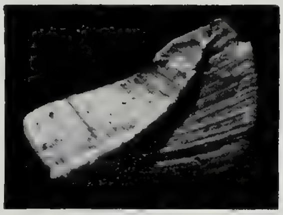
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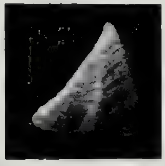
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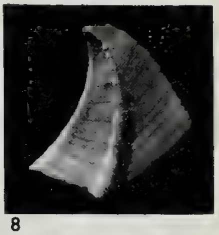
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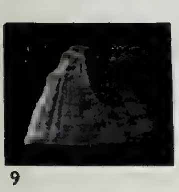
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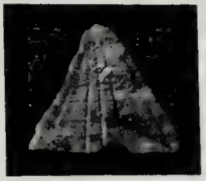
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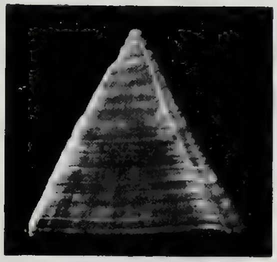
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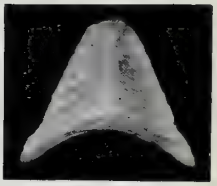
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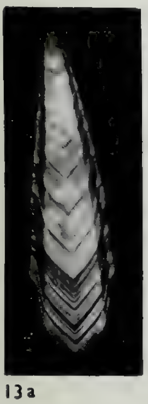
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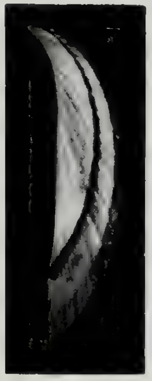
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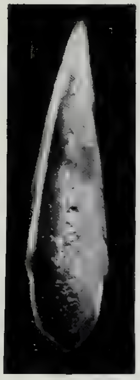
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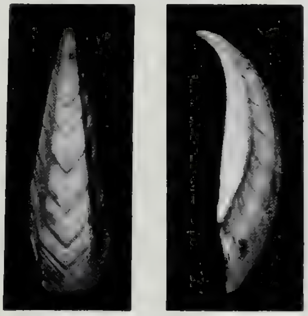
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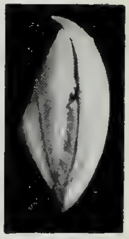
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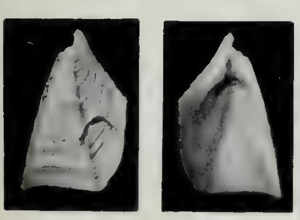
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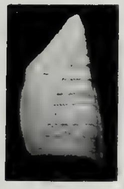
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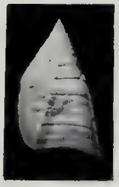
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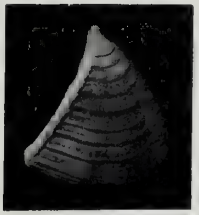
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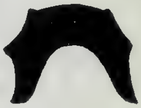


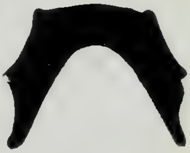

20a-b

PLATE 3

Arcoscalpellum hubrichti sp. nov. Page 363

FIG. 1. Tergum (right). Outer view, ×2 diam. A1. Paratype. 6074PRI.

FIG. 2. Tergum (right). *a*, outer view; *b*, inner view, ×2 diam. A3. MSU 1324.

FIG. 3. Tergum (right). Outer view, ×2 diam. A1. In.64439.

FIG. 4. Upper latus (left). Outer view, showing well developed growth beyond the umbo, ×2 diam. A7. Paratype. In.64443.

FIG. 5. Upper latus (right). Outer view, ×2 diam. A7. Paratype. In.64444.

FIG. 6. Carinal latus (right). Outer view, ×2 diam. A7. Paratype. In.64440.

FIG. 7. Carina. Side view of apical part, ×2 diam. A1. Paratype. 60873*a*PRI.

FIG. 8. Carinal latus (right). *a*, outer view; *b*, inner view, ×2 diam. A7. Paratype. In.64441.

FIG. 9. Carinal latus (left). Outer view, ×2 diam. A7. Paratype. In.64442.

Arcoscalpellum bakeri sp. nov. Page 367

Maastrichtian, Ripley Formation.

FIG. 10. Carina. *a*, outer view; *b*, side view; *c*, inner view, ×2 diam. M4 : Oktibbeha County, Mississippi. Holotype. In.64446.

FIG. 11. Transverse sections of carina taken at, *a*, c. 5·0 mm and *b*, c. 18·0 mm from the apex ×5 diam. Paratype. In.64448.

FIG. 12. Carina. *a*, outer view; *b*, inner view, ×4 diam. M3. Paratype. In.64447.

FIG. 13. Tergum (right). Outer view, ×4 diam. M2. Paratype. In.64449.

Arcoscalpellum campus sp. nov. Page 369

Maastrichtian, Middle Ripley Formation.

FIG. 14 Carina. *a*, outer view; *b*, side view, ×2 diam. M5 : Oktibbeha County, Mississippi. Holotype. In.64452.

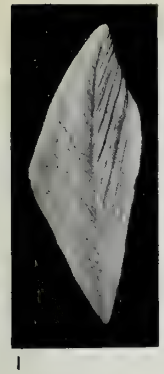
FIG. 15. Scutum (left). *a*, outer view; *b*, inner view, ×4 diam. M5. Paratype. MSU 1328.

FIG. 16. Carinal latus (right). *a*, outer view; *b*, inner view, ×4 diam. M4. Paratype In.64453.

Arcoscalpellum withersi sp. nov. Page 371

Maastrichtian, Ripley Formation.

FIGS 17–18. Rostral latera (left & right). Outer view, ×4 diam. M5. Paratypes. In.64454–64455.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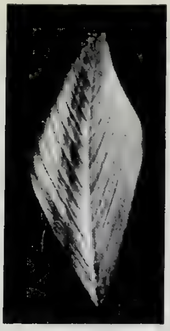
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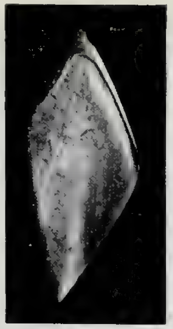
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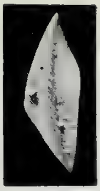
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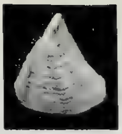
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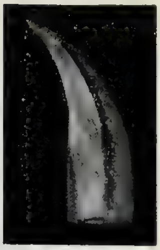
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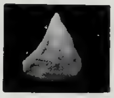
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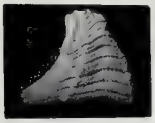
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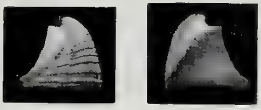
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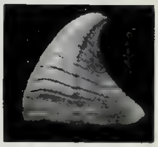
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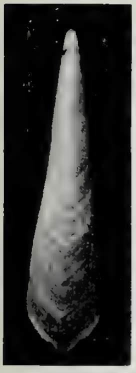
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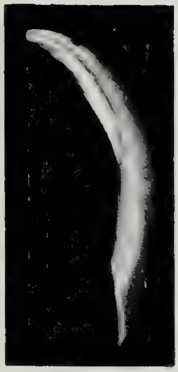
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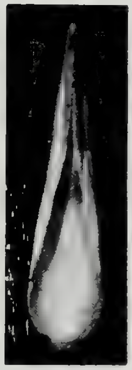
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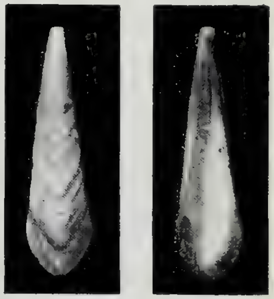
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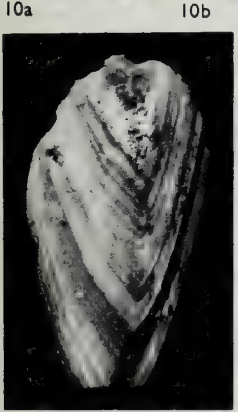
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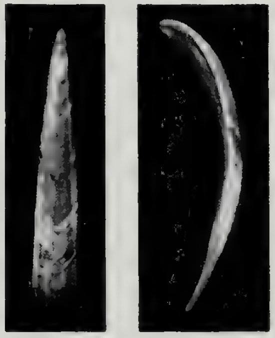
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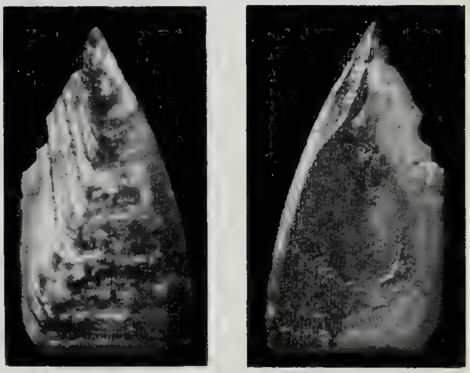
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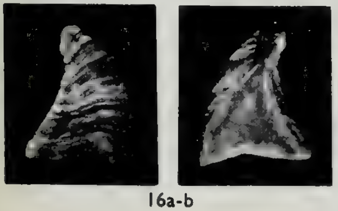
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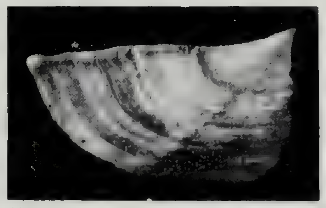
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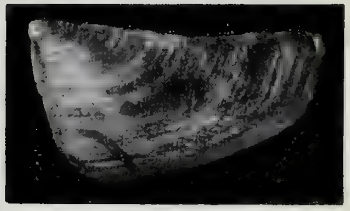
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PLATE 4

Arcoscalpellum campus sp. nov. Page 369

Fig. 1. Scutum (left). Outer view, ×4 diam. M5. Paratype. In.64450.

Fig. 2. Tergum (left). *a*, inner view; *b*, outer view, ×4 diam. M5. Paratype. In.64451.

Fig. 3. Tergum (left). Outer view, ×4 diam. M4. Paratype. MSU 1329.

Fig. 4. Transverse section of carina, In.64452, at c. 4·0 mm from the apex, ×6 diam.

Arcoscalpellum withersi sp. nov. Page 371

Fig. 5. Carina. Outer view, ×2 diam. OC.7. Paratype. MSU 1330.

Fig. 6. Carina. *a*, outer view; *b*, side view; *c*, inner view, ×2 diam. M3 : Oktibbeha County, Mississippi. Holotype. In.64456.

Fig. 7. Transverse sections of carina, at, *a*, c. 6·0 mm and *b*, c. 11·0 mm from the apex, ×5 diam. M3. Paratype. In.64463.

Fig. 8. Scutum (right). Outer view, ×2 diam. M4. Paratype. In.64459.

Fig. 9. Scutum (right). *a*, outer view; *b*, inner view, ×2 diam. M3, Paratype. MSU 1331.

Fig. 10. Tergum (right). Outer view, ×2 diam. M2. Paratype. MSU 1332.

Fig. 11. Tergum (left). Outer view, ×2 diam. M3. Paratype. In.64457.

Fig. 12. Tergum (left). Outer view, ×2 diam. M2. Paratype. MSU 1425.

Fig. 13. Scutum (left). Outer view, ×2 diam. M4. Paratype. MSU 1426.

Fig. 14. Carinal latus (right). *a*, outer view; *b*, inner view, ×4 diam. M4. Paratype. In.64461.

Fig. 15. Upper latus (right). Outer view, ×4 diam. M4. Paratype. In.64462.

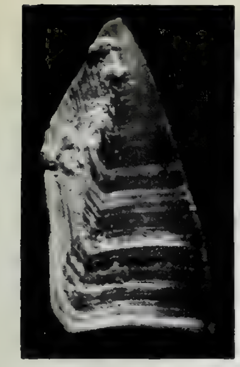
Virgiscalpellum gabbi gabbi (Pilsbry) Page 374

Maastrichtian, Ripley and basal Prairie Bluff Formations.

Fig. 16. Upper latus (right). Outer view, ×4 diam. OC.1. In.64474.

Fig. 17. Carina. *a*, outer view; *b*, side view, ×2 diam. M8. MSU 1334.

Fig. 18. Carina. *a*, side view; *b*, inner view, ×2 diam. OC.1. In.64464.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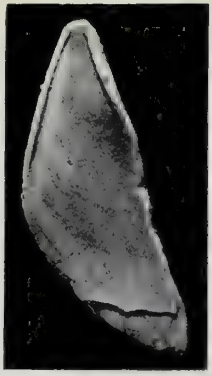
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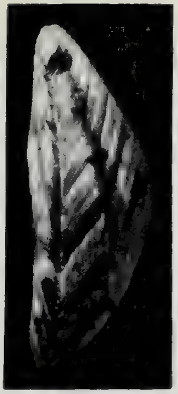
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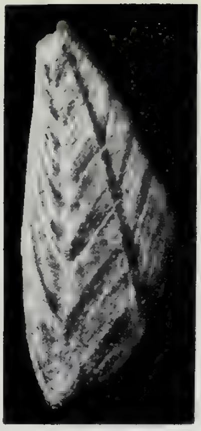
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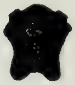
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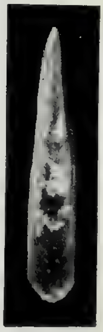
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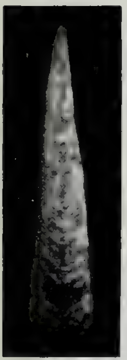
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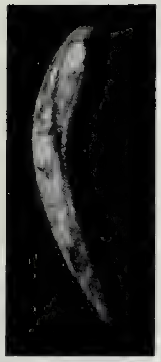
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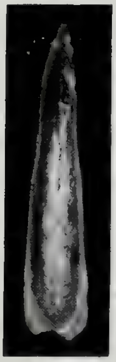
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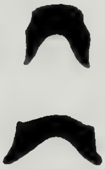
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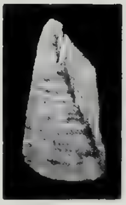
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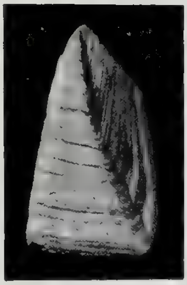
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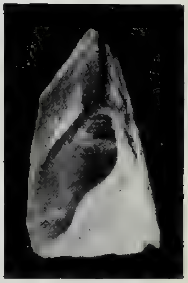
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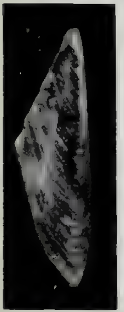
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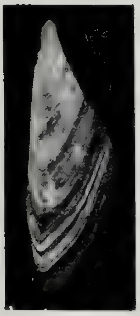
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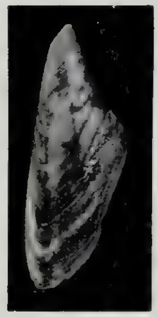
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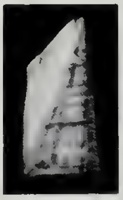
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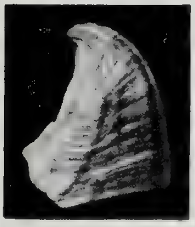
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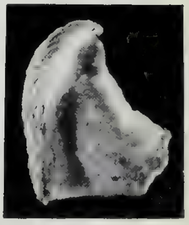
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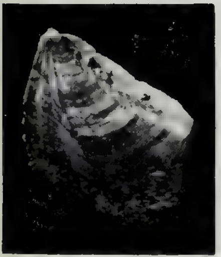
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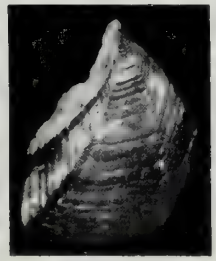
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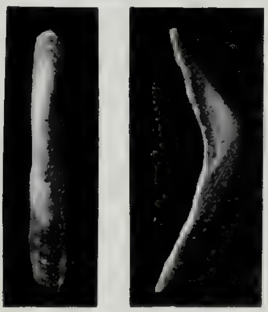
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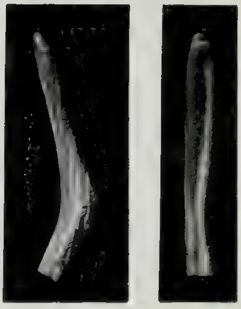

18a-b

PLATE 5

Virgiscalpellum gabbi gabbi (Pilsbry) Page 374

FIG. 1. Tergum (left). *a*, outer view; *b*, inner view, ×2 diam. M2. In.64472.
FIG. 2. Tergum (left). Outer view, ×2 diam. M2. MSU 1335.
FIG. 3. Scutum (right). *a*, outer view; *b*, inner view, ×2 diam. M2. Paratype. In.64467.
FIG. 4. Tergum (left). Outer view, ×2 diam. OC.2. In.64469.
FIG. 5. Rostral latus (left). Outer view, ×4 diam. M3. Paratype. MSU 1337.
FIG. 6. Rostral latus (left). Outer view, ×2 diam. M3. Paratype. In.64475.
FIG. 7. Scutum (left). Outer view, ×2 diam. M2. Paratype. In.64470.
FIG. 8. Carinal latus (right). Outer view, ×4 diam. OC.1. Paratype. In.64473.
FIG. 9. Transverse sections of carinae: *a*, open lower limb 4·0 mm from umbo, In.64465; infilled lower limb 8·0 mm from umbo, In.64466. ×5 diam. M2.
FIG. 10. Carina. *a*, side view; *b*, inner view, ×2 diam. With the umbo and part of the lower limb infilled. M8. MSU 1416.
FIG. 11. Scutum (right). Outer view, ×2 diam. M2. MSU 1336.

Virgiscalpellum sp. Page 379

Upper Senonian, basal Annona or upper Coffee Formation.

FIG. 12. Scutum (right). Outer view, ×4 diam. OC.6 : Clay County, Mississippi. In. 64476.

Virgiscalpellum sp. Page 379

Maastrichtian, Upper Ripley Formation.

FIG. 13. Tergum (left). Outer view, ×4 diam. OC.3 : Oktibbeha County, Mississippi. In.64477.

Virgiscalpellum gabbi gabbi (Pilsbry) Page 374

FIG. 14. Carina. *a*, outer view; *b*, side view; *c*, inner view, ×2 diam. With thickened lateral margins. OC.1. In.64487.

Virgiscalpellum gabbi apertus sub-sp. nov. Page 378

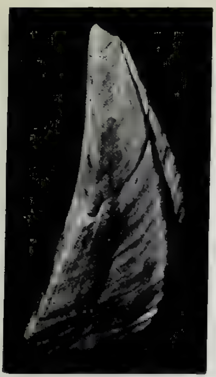
Maastrichtian, Ripley and basal Prairie Bluff Chalk.

FIG. 15. Carina. *a*, outer view; *b*, side view; *c*, inner view, ×2 diam. OC.4 : Oktibbeha County, Mississippi. Holotype. In.64478.

Brachylepas angulosa sp. nov. Page 380

Maastrichtian, Ripley Formation.

FIG. 16. Rostrum. *a*, outer view; *b*, side view; *c*, inner view, ×4 diam. M4 : Oktibbeha County, Mississippi. Holotype. In.64479.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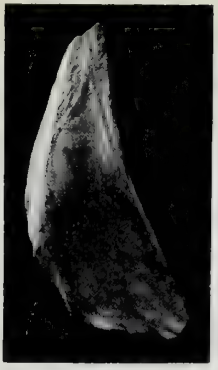
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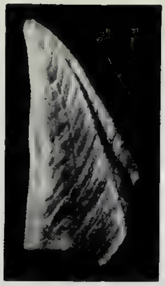
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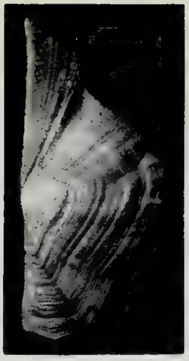
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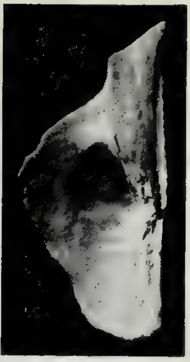
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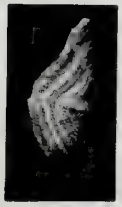
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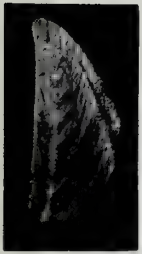
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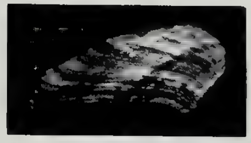
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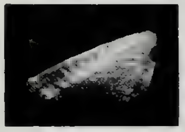
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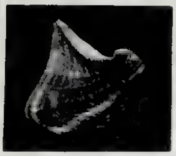
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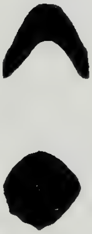
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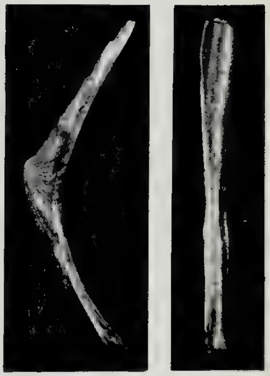
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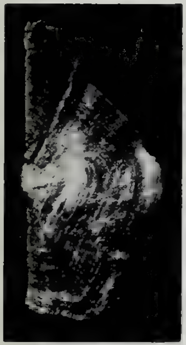
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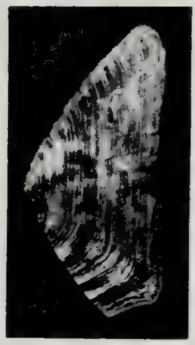
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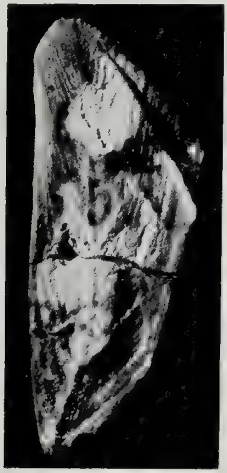
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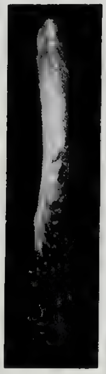
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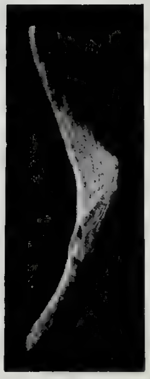
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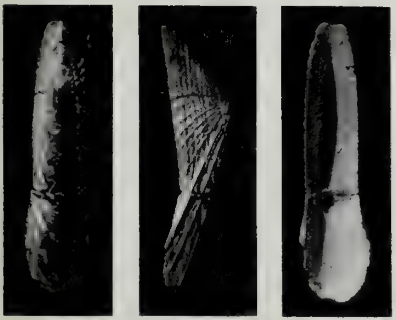
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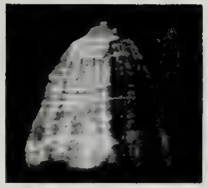
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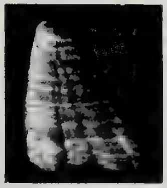
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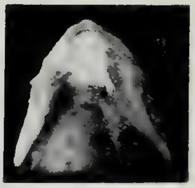
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FENESTRATE BRYOZOA FROM THE VISEAN OF COUNTY FERMANAGH, IRELAND

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-4 OCT 1973
NATURAL HISTORY

R. TAVENER-SMITH

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GEOLOGY Vol. 23 No. 7
LONDON : 1973

FENESTRATE BRYOZOA FROM THE VISEAN OF COUNTY FERMANAGH, IRELAND

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- 4 OCT 1973
NATURAL HISTORY

BY

R. TAVENER-SMITH
Queens University, Belfast

Pp 389-493; 26 *Plates*, 5 *Text-figures*

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FENESTRATE BRYOZOA FROM THE VISEAN OF COUNTY FERMANAGH, IRELAND

By R. TAVENER-SMITH

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SYNOPSIS

This report deals with silicified fenestrate bryozoa from D_1 limestones at Carrick Lough, County Fermanagh. Thirty-two species belonging to eight genera are described, including two new species and three sub-species. The genus *Septopora* is recorded from Ireland for the first time.

Sedimentary characteristics suggest that the bryozoans are part of a drift assemblage accumulated in de-oxygenated conditions in water of moderate depth. There are indications that the fenestrate colonies originally grew in a shallower and better aerated environment on the flanks of reef mounds.

A review of the present situation in fenestellid taxonomy suggests a need for increased use of zooecial, as opposed to zoarial, characteristics, and for the use of accepted biometric methods in comparing samples of numerical data. Statistical information included in systematic descriptions is arranged so as to facilitate the latter aim.

I. INTRODUCTION AND ACKNOWLEDGEMENTS

This bulletin contains systematic descriptions of fenestrate bryozoa from an argillaceous limestone sequence at Carrick Lough, County Fermanagh. The geographic position of the collecting locality, which is about three miles north-west of Derrygonelly village, and about eleven from Enniskillen in the same direction, is shown in Text-figs 1 & 3.

Etching of limestone blocks from this locality yielded a silicified fauna which included a profusion of well preserved fragments of fenestrate bryozoa with a range of form exceeding that shown by any comparable collection in the British Isles or, indeed, in all Europe. A unique opportunity was therefore presented to study the structure and systematics of this common, though neglected, group of fossils. Silicified brachiopods from the same general locality and horizon have been described in an earlier Bulletin of this series (Brunton 1966).

Identification of the fenestrate fossils necessarily involved comparison with type material in other collections, and in this connection I am indebted to the late Dr H. Dighton Thomas of the British Museum (Natural History); to Dr J. S. Jackson of the National Museum of Ireland, and to Mr M. Mitchell of the Geological Survey Museum, who provided access to material in their care. In addition, specimens were kindly loaned by the Curators of the United States National Museum; the Sedgwick Museum, Cambridge; the Hunterian Museum, University of Glasgow, and by Dr R. D. Wilson of the Scottish Office, H.M. Geological Survey.

I also wish to thank Messrs C. D. Kemp, Queen's University, and D. H. McNally, Ministry of Agriculture, for useful discussions on statistical aspects of the work; Dr Helen Duncan, U.S. National Museum, for making reference books available on extended loan; and Professor Alwyn Williams for critically reading the manuscript.

II. STRATIGRAPHY

Although the ground between lower Lough Erne and Lough Melvin has not been mapped since the work leading to the Geological Survey publications of 1885, neighbouring country to the north and south has received more recent attention (Simpson, 1954; Oswald, 1955; George & Oswald, 1957). In these areas the Carboniferous stratigraphy is quite well known, and by reference to it the horizon of the collecting locality at Carrick Lough can be determined.

In Leitrim and Sligo the youngest calcareous formation mapped by Oswald is the massive, chert-bearing Dartry Limestone, dated as D_1 on palaeontological evidence (Oswald 1955; 180). Below this is the Glencar (or Upper Calp) Limestone, with its distinctive limestone-shale lithology, also considered by Oswald to be of D_1 age. The contact between these formations is gradational and both contain reef structures which are, however, commonest in the Dartry Limestone. The latter generally forms a prominent topographic feature, and can be traced without difficulty from Sligo and Leitrim into south Fermanagh and the vicinity of Carrick Lough. Hills on the south side of that lough are part of a locally developed reef complex in a lateral extension of the Dartry, while on the lough shore shales and limestones of Glencar-type are exposed. The junction between the two formations is transitional, as in Oswald's area. The fossil assemblage described in this Bulletin was obtained from beds of argillaceous limestone intercalated with shale below the reef, and is therefore of late Glencar age in terms of the Sligo succession.

Further correspondences are also evident between the succession around Carrick Lough and those of the better known Carboniferous areas to west, north and south. For instance, the country between the collecting locality and the shore of Lough Erne, some three miles away, is underlain by thick, black shales which must be lateral equivalents of the Bundoran and Benbulben (Calp) Shales of the Donegal and Sligo coasts. The Calp Sandstone (Mullaghmore, Kildoney or Mountcharles Sandstones of Oswald 1955, and George & Oswald 1957) is present within these black shales, though poorly exposed and probably thinner than to the west and north. It outcrops about a mile north-west of Derrygonelly village, and the surveyors of 1885 also recorded it in the vicinity of Monea.

Dark, thick-bedded limestones with thin shale partings are to be seen in many roadside quarries close to the south shore of Lough Erne, between Ely Lodge and Tully Point. They dip beneath the black shales and are locally the lowest visible Dinantian strata. This formation corresponds exactly in lithology and stratigraphic position with the Ballyshannon Limestone of Oswald, which underlies a strip of country a few miles to the west, between Belleek and the coast. The Ballyshannon Limestone of that vicinity is virtually continuous along the strike with Simpson's Pettigo Limestone to the north-east, with which it must be correlated. The Ely Lodge–Tully Point limestone on the south side of Lough Erne is also, no doubt, a lateral equivalent of the Pettigo Limestone, though there is no sign to the south of the Lough of the thick arenaceous formations which underlie the limestone in the Kesh–Omagh area and form the base of the Dinantian there.

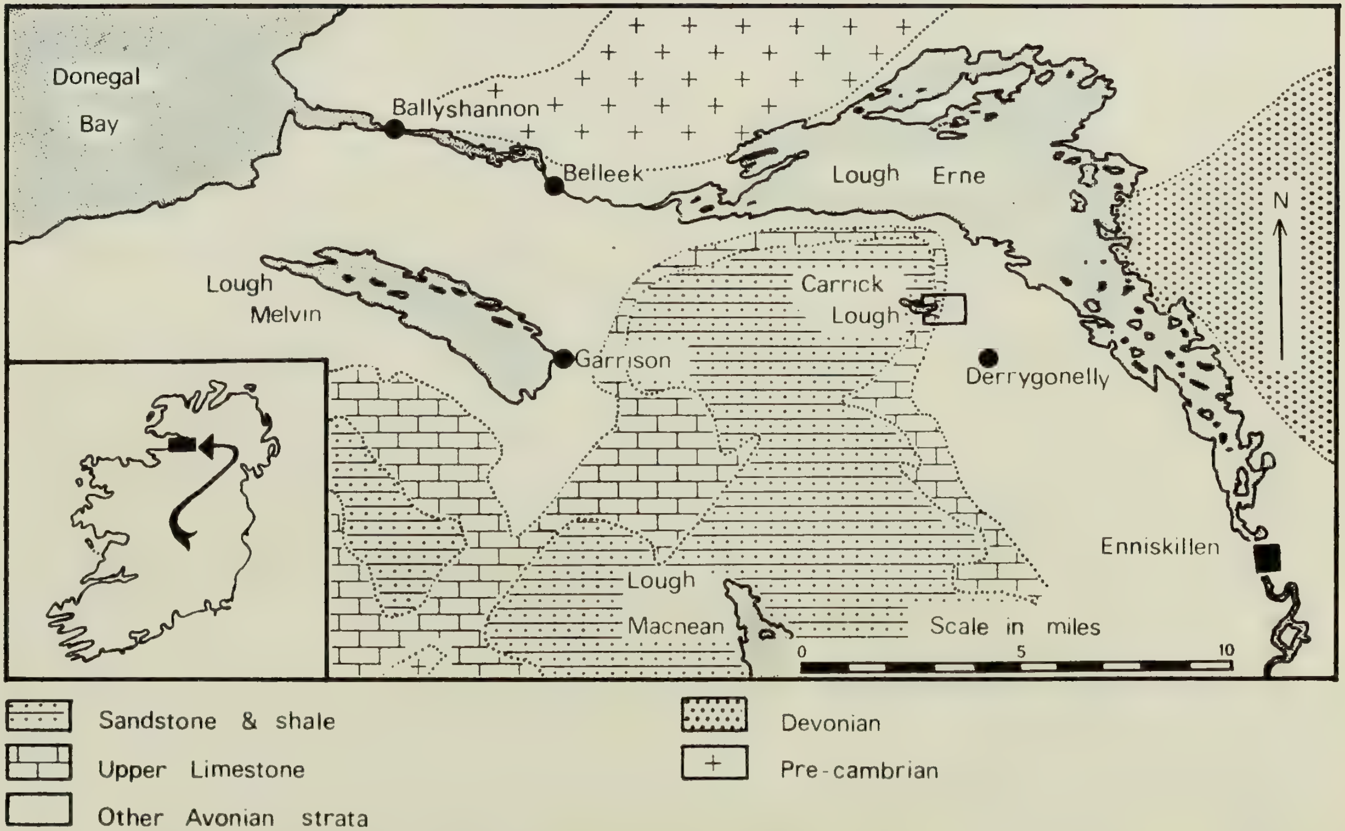
Donegal
Bay
Ballyshannon
Belleek
Lough Erne
N
Lough
Melvin
Carrick
Lough
Garrison
Derrygonelly
Enniskillen
Lough
Macnean
Scale in miles
0
5
10
Sandstone & shale
Upper Limestone
Other Avonian strata
Devonian
Pre-cambrian

FIG. 1. Generalized map showing the geographical and geological setting of Carrick Lough. Inked rectangle near the lough indicates the limits of the area shown in Fig. 3.

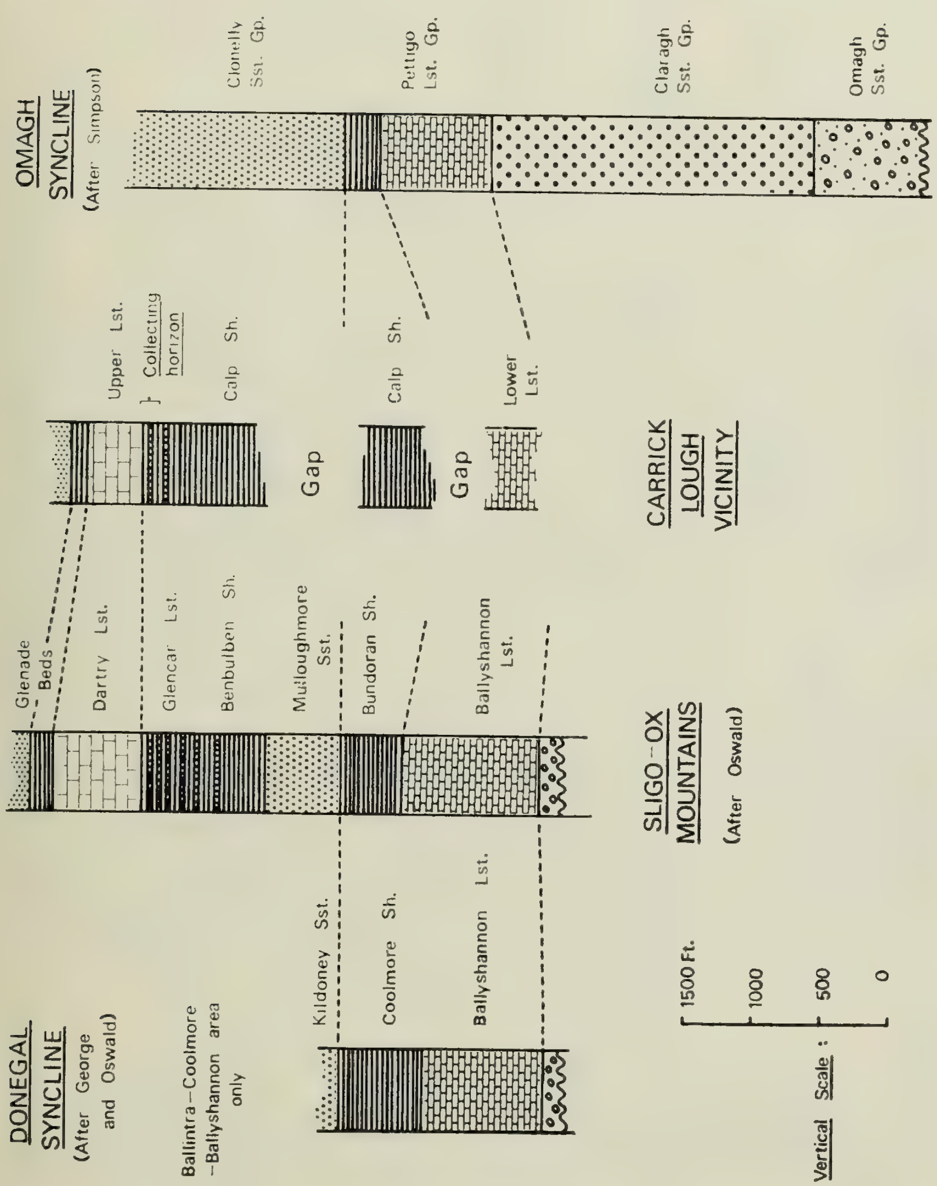
DONEGAL SYNCLINE
(After George and Oswald)
Ballintra–Coolmore –Ballyshannon area only
Kildoney Sst.
Coolmore Sh.
Ballyshannon Lst.
SLIGO–OX MOUNTAINS
(After Oswald)
Glenade Beds
Dartry Lst.
Glencar Lst.
Benbulben Sh.
Mulloughmore Sst.
Bundoran Sh.
Ballyshannon Lst.
CARRICK LOUGH VICINITY
Upper Lst.
Collecting horizon
Calp Sh.
Gap
Calp Sh.
Gap
Lower Lst.
OMAGH SYNCLINE
(After Simpson)
Clonelly Sst. Gp.
Pettigo Lst. Gp.
Claragh Sst. Gp.
Omagh Sst. Gp.
Vertical Scale :
1500 Ft.
1000
500
0

FIG. 2. Relationship of the stratigraphic succession in the Carrick Lough vicinity to that in other parts of north-west Ireland. In some parts of Donegal the succession is very arenaceous in the lower part and much thicker than indicated above.

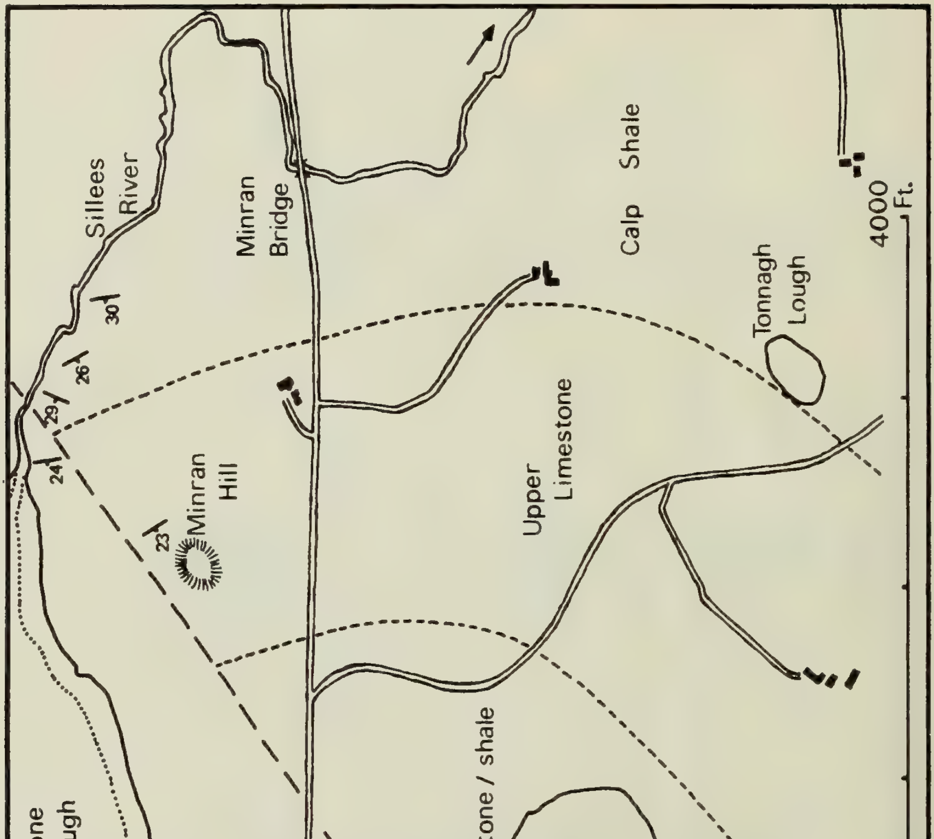
Sillees River
Minran Bridge
Calp Shale
4000 Ft.
0
Tonnagh Lough
30
26
29
24
23
Minran Hill
Upper Limestone
Bunnahone Lough
Spectacle Lough
Sandstone / shale
Sandstone / shale
Fault
Fault
Ruined Church
Carrick Lough
60
32
34
Collecting locality
N

FIG. 3. Situation of the collecting locality at Carrick Lough. Dotted lines indicate present water levels in the loughs, following recent drainage operations.

Text-fig. 2 relates the succession around Carrick Lough to those of neighbouring areas, as indicated by recent work. In view of the general correspondence between them, and the position of the collecting horizons in the sequence at Carrick Lough, there is little doubt that the fossil assemblage described in this report is of early D_1 age.

The beds from which collections were made form an inconspicious series of exposures at the foot of a steep, wooded bluff about half-way along the south side of Carrick Lough. They are also exposed on the adjacent beach, which has formed since the water level in the lake was lowered by deepening the course of the Sillees River. The strike is to the north-east or east-north-east, roughly at right angles to the trend of the shore, and the beds dip north-west, generally at from 25 to 35 degrees.

The strata are essentially alternations of shale and argillaceous limestone, though the proportion between these constituents is not constant. At the south-east (stratigraphically lower) end of the section the beds are mainly mid-grey to buff weathering shale with thin (2 to 6 in.) limestone bands. Ascending the succession the latter increase in number and thickness until, at the north-west end, shale is only present as thin partings and there is a passage into the massive, pale, reef limestone of the succeeding formation. In the lower part of the section limestone bands commonly weather out of the shale as flaggy ledges, and this is particularly noticeable on the wide beach. Beds in this situation have been etched by the peaty water of the lough and commonly show prominent, silica-rich, upper and lower crusts separated by a deeply-etched, pale-weathering, calcareous part from which silicified fossils protrude.

Blocks of limestone from beds of the kind described were collected at five separate horizons in a thickness of 240 ft of strata. These were respectively at 24–30 ft; 47 ft; 87–99 ft; 110–117 ft and 224–234 ft vertically below the base of the reef which locally represents the Dartry–Glencar contact. Blocks from the four lower horizons were of a dark, flaggy, pyritous nature, while those from the uppermost level were fine-grained, dove-grey, limestone. Such beds, intercalated among predominant argillaceous limestones and shales in the upper part of the section, may represent the lower extremities of lenticular deposits of wave-broken debris which accumulated locally on the flanks of reef mounds, and extended at their lower extremities into deeper water.

III. TREATMENT OF SAMPLES

About fifteen hundredweight of limestone blocks were collected and etched, using the following technique. Blocks were placed in deep polythene basins and covered with a 20% solution of hydrochloric acid and hot water. At forty-eight-hour intervals the spent liquor was siphoned off and the blocks carefully washed with clean, warm water. After this the basins were re-filled with acid and hot water. The method was found to promote a continuous and vigorous action until etching was completed.

The nature of the insoluble residue left after etching was found to vary considerably. Argillaceous limestone from the lower collecting horizons yielded relatively large amounts of black sludge, whereas the reef-type limestone produced very little. Some blocks, with prominently weathering fossils and a promising exterior appearance, proved on etching to contain slabby masses of spongy chert, and the fossil yield was disappointing.

The etched fossils and associated muddy residue were, as far as practicable, carefully removed whenever the acid was changed. It was found possible to eliminate most of the mud from the mixture by gently 'panning' it, using a wide, shallow dish and adding clean water at intervals. After this the remaining residue, consisting mostly of fossil material, was transferred a little at a time to petrie dishes for more thorough washing to remove acid traces and mud particles. Larger specimens with mud still adhering were immersed in 100 vol. hydrogen peroxide to which a little caustic soda was added. The ensuing reaction cleansed them of even the finest muddy accretions, and the specimens were then placed on blotting paper to dry, prior to preliminary sorting.

Examination showed the silicified fossils to be delicate, fragile and commonly hollow. Replacement apparently progressed into the fossils from the exterior, for the outer surfaces of many faithfully retain the sculptural detail of the originals, while internal structures are poorly preserved or absent, due to the failure of replacing solutions to penetrate into the axial parts. It is evident from thin sections of limestone that silicification is not necessarily uniform over the whole surface of a fossil. Where replacement was only partial, etching must have resulted in the collapse of a formerly complete fossil into several pieces. This has undoubtedly contributed something to the fragmented nature of the fauna, though there is good reason to believe that breakage was largely of pre-depositional occurrence.

The original skeletal material has been replaced by either chalcedony or quartz. In the former case the internal structure may be well preserved, but it is generally lost where replacement is by quartz. This occurs either as spongy-textured masses, or in a relatively coarsely crystalline form. Replacements of the second kind may extend into the matrix, so that small adventitious masses of quartz adhere to a fossil. These can sometimes be removed with a mounted needle or forceps, though not without risk of damage. A few of the larger brachiopod valves, and secondarily thickened branches of *Polypora* and *Ptylopora* showed crude rings of beekite which may obscure a fossil almost beyond recognition. Fortunately this is rare.

IV. NATURE AND SIGNIFICANCE OF THE FAUNA

Commonest among fossils in the residues are fragmented colonies of fenestrate bryozoa. They are followed by small brachiopods (chiefly productids), non-fenestrate bryozoa and sponge remains, in that order of abundance. With these groups are associated small numbers of simple, rugose horn-corals, lamellibranchs, gastropods and trilobites. Earlier work on silicified faunas (Whittington & Evitt 1953 : 7; Newell 1953 : 172) has shown that certain groups of fossils are more liable to replacement in this way than others, so that an etched fauna may give a distorted impression of the original assemblage from which it was derived. Comparison with unsilicified fossils in strata at the collecting locality suggests, however, that in this case the etched fauna provides a reasonably close indication of the original fossil content of the rocks, both in the groups present and their relative proportions.

The predominant constituents of the etched residues are, therefore, bryozoa and brachiopods. In palaeontology this is a recurring association, and there is ample evidence that in many cases representatives of the two phyla shared a common environment (e.g. Sarle 1901 : 286; Duncan 1957 : 788). In spite of this, it seems probable that the Carrick Lough fauna does not represent a benthonic community, that is, a former life assemblage fossilized more or less *in situ*. Reasons for this belief are given in the following paragraphs.

The attitude of bryozoan fronds, in partly etched blocks and in thin sections, shows that the vast majority did not occupy positions of growth at the time of burial. On the contrary, they lie approximately in the plane of bedding, and rest upon one another in a close-woven tangle of organic debris. This is particularly notable in dark, muddy, pyritous limestones from the lower collecting horizons. The size and shape of fenestrate fronds seen on polished surfaces and in acetate peels from limestone blocks make it clear that fragmentation of the colonies had already taken place before consolidation of the sediment. The breakage may have been caused by predaceous organisms or the action of turbulent water, but is unlikely to have been due to re-working by burrowing organisms, for sedimentary laminae are well preserved in the rocks.

Acetate peels and polished surfaces also show the presence of disoriented fistuliporid colonies and disarticulated brachiopod valves, testifying to the movement of organic debris by wave or current action. Signs of turbulence in the depositional environment are not lacking, and take the form of minor bedding-plane irregularities and the presence, in dark, argillaceous limestone, of ooliths and intraclasts of pale, fine-grained reef material. Schwarzacher (1963) was able to demonstrate bottom current effects by means of oriented crinoid stems in beds of similar age and lithology in Sligo.

Argillaceous and bituminous limestone blocks, of the kind obtained from all but the highest collecting horizon, contain large numbers of fenestrate fragments associated with productoid brachiopods and an abundance of silicious sponge spicules. This is unlikely to represent a life association. Newell (1953 : 197) found silicious sponges to be the chief indigeneous faunal element in deep water bituminous limestones and shales from the Delaware Basin. In association with the spicules were productoid and other brachiopods thought to have tolerated relatively de-oxygenated conditions and the presence of suspended mud in the water. Argillaceous limestones and shales of the Carrick Lough section bear a close lithological resemblance to the basin facies of the Delaware region, and probably originated in a similar environment. If present day ecology is an acceptable guide, basin-type conditions would not favour the growth of branching and fenestrate bryozoa, for contemporary genera of this kind prefer well-aerated water and do not tolerate a high rate of sedimentation (Stach 1936, Lagaaij & Gautier 1965). In addition, the depth of water may well have been too great. Schwarzacher (1961 : 1502) concluded that in the Sligo area basin-type sediments adjacent to reef mounds formed in water at least 400 ft deep, whereas present day fenestrate bryozoa flourish best at depths of 80 to 200 ft (Stach 1936 : 62; Lagaaij & Gautier 1965 : 54 and Chart I). On sedimentological grounds Elias (1937 : 428) concluded that fenestellid bryozoa in the Big Blue Series, Kansas, grew at depths varying from 75 to 160 ft.

In view of these considerations it is probable that bryozoan remains in the etched residues were moved to some extent prior to their final deposition and burial. But although it is apparent from their attitude and condition that the colonies did not grow in the situations where they are now found, the size of fragments and common preservation of delicate structures indicate that they were not carried far from the areas of growth. For reasons already given it seems unlikely that fenestrate bryozoa would have flourished in a sea-floor environment such as that represented by dark, bituminous limestones or shales, and an alternative habitat must be sought. Fortunately there is an indication of its whereabouts.

In the Carrick Lough fauna the largest fenestrate fragments were invariably obtained from pale, reef-type beds of the topmost collecting horizon. From their lithology, position and thickness it is probable that these represent the lower extremities of lenticular apron breccias which extended away from reef mounds and became intercalated with muddy deposits on the adjacent sea floor. The recovery of larger fenestrate fragments from these beds suggests that they were relatively closer to the bryozoan growth area than the muddy limestones of the lower collecting horizons. This, together with the likelihood that the bryozoan debris was carried *down* the sloping reef flanks rather than up them, makes it probable that the original habitat was upon locally existing reefs. In that situation the water would have been better aerated, and environmental conditions would have been generally more favourable than in the deeper, de-oxygenated water of the surrounding sea bed.

Records from many parts of the world relating to occurrences varying widely through time show that bryozoa have commonly been, and still are, associated with reef structures (e.g. Lowenstam 1950, Magdefrau 1933, Theodorovich 1941, Newell 1953). In addition, it has been found that whereas encrusting, massive and stoutly ramose forms inhabit the strongly turbulent water of reef flats, the fore-reef slopes commonly support a luxurient growth of slenderly branching, pinnate and fenestrate colonies. It seems quite possible, therefore, that the masses of drifted bryozoan remains in the limestones from Carrick Lough were derived from the slopes of adjacent reef structures, where these organisms may formerly have lived in great profusion. It is likely that they were fragmented before or after death (mainly the latter) by predatory organisms and perhaps by wave action, and the remains slowly moved into deeper water by gravity and current action. In the somewhat de-oxygenated conditions of the sea bed at the foot of the reef slope, where siliceous sponges and muddy water brachiopods formed the indigeneous fauna, the bryozoan debris accumulated and was buried in relatively large amounts.

V. TAXONOMY

The taxonomy of fenestrate bryozoans presents some unusual problems. This is partly the result of a strong tendency for intra-specific morphological variation, and partly because almost all specimens are small fragments of complete colonies. A wide range of zoarial construction has, for example, been demonstrated (Tavener-Smith 1965) within a single species of *Ptilofenestella*, and it is common knowledge that fenestellid colonies may differ in structure from one part to another. Such variations may be due to differences of age or ecology, or to growth aberrations (Elias & Condra 1957 : 59). *Post mortem* fragmentation of zoaria has, therefore, added greatly to the difficulties facing taxonomists in dealing with this group, for many species have been founded on single small fragments.

Fenestellid genera are based primarily on zoarial shape and the morphological character of branches in mature parts of colonies. Specific differences, on the other hand, commonly rest on variations of meshwork texture, and this is particularly so in *Fenestella*. Ulrich (1886, 1890) popularized the technique of making standard measurements of meshwork dimensions in fenestrate zoaria and using these for taxonomic purposes. He made no allowance for intra-specific variation, however, and in this respect his concept of species was inadequate. The Russian workers Nekhoroshev and Nikiforova, in a series of publications from 1926 onward, recognized the importance of structural variation within a species and sought to express it in numerical form. The arrangement they adopted has become known as the 'meshwork formula' (Condra & Elias 1944 : 56–57), or 'micrometric formula' (Miller 1961 : 224), and states the range of the number of branches, dissepiments, apertures and carinal nodes per unit distance in a specimen or series of specimens. This attempt to give quantitative expression to intra-specific meshwork variation, and the regular consideration of this factor in comparing data, marked a considerable advance on previous taxonomic practice. Condra & Elias (1944) introduced the technique to western workers and made great use of it themselves. However, though the micrometric formula may be of use in indexing fenestellid species on the basis of their meshwork characteristics, it has been shown (Tavener-Smith 1966b) quite unsatisfactory in taxonomy. From a biometric stand-point the formula is a crude device and completely inadequate as a basis for the comparison of numerical data. It is not therefore surprising that it commonly yields ambiguous results when used in that way. Furthermore, many formulae are founded on single, small meshwork fragments, and in such cases may fail to reflect the range of structural variation even within the colony to which the fragment belonged. Though the wish to indicate the known limits of morphological variation in defining a species and to utilize this factor in comparing samples was conceptually correct, the application of the micrometric formula towards this end has created much confusion.

Because specific differentiation in *Fenestella* and its allies has been largely a matter of meshwork structure, a feature that may vary even within a colony, and because species have commonly been founded on small fragments, it is not surprising that large numbers have been erected. There are now more than 500 species in *Fenestella* alone. Their constantly increasing number causes mounting difficulty in the identification of new material, and several schemes have been devised in an attempt to provide a more manageable grouping. Simpson (1895 : 500) divided the species of *Fenestella* into seven categories based on the nature of the carina, but his scheme was poorly founded and met with little success. Elias (1937) suggested four provisional groups of Pennsylvanian and Permian species, using the number of zooecial apertures per fenestrule and the number of rows of carinal nodes. Trizna (1939 : 103–111), and later Shulga-Nesterenko (1941 : 44), proposed comparable patterns for Permian *Fenestella* from Russia, while Elias & Condra (1957 : 67–72) suggested an elaborate classification of *Fenestella* from the Pennsylvanian and Permian of the Glass Mountains, Texas. This comprised thirteen groups based primarily on the arrangement of carinal nodes, number of zooecia per fenestrule and the fenestrule length. Such classifications have a certain pragmatic value in that they facilitate the comparison of new material with the large number of species now in the literature. In doing so they fulfill a similar function to the micrometric formula when used for indexing purposes. These schemes are, however, basically a palliative, not a cure. They do nothing to stem the ever increasing tide of new species, but attempt temporarily to render it more manageable.

It is likely that a major factor in the proliferation of fenestellid species has been the use of meshwork dimensions as the main basis of classification. Such features seem an obvious choice for the purpose, but earlier experience suggests that they may not be the best. Writing seventy years ago about the classification of another group of fenestrate bryozoa, Waters (1896 : 255) commented: 'Our knowledge of the Mediterranean Reteporae is most unsatisfactory, as so many specific names have been given on account of slight differences in the nature of the reticulation . . . it has become quite clear that this is not a satisfactory character', for classificatory purposes. Waters was subsequently proved right (Harmer 1934), and the situation of which he wrote is also that afflicting the taxonomy of the Fenestellidae at the present time.

Among early workers it was the custom to classify bryozoa according to their zoarial shape, an outlook reflected in Canu's (1900 : 336) dictum that, 'L'individualité bryozoaire est le zoarium.' Since that time workers on living and fossil Cheilostomata have laid increasing stress upon the characteristics of the zooid rather than those of the colony. This change of emphasis, in keeping with the view expressed earlier by Waters, has become so pronounced that Lagaaij & Gautier (1965 : 39) deliberately misquoted Canu to the effect that, 'L'individualité bryozoaire est le *zooecium.*' They continued by saying that, 'It is often not the size or shape of the colony, but rather the characters of the individual zooecium that determine the identity of species of cheilostomatous bryozoa.' In the case of the Fenestellidae also it is reasonable to suppose that morphological characteristics relating to zooecial chambers, or to the wall structure, will eventually prove of greater taxonomic worth than zoarial features. The former are likely to have been subject to tighter genetic control, and should, therefore, have greater potential value for specific differentiation. The latter, being essentially a framework maintaining the zooecia in suitable life positions, would predictably be more subject to ecological influence, and perhaps therefore more variable in development. Variation in structures formed by supporting tissue is certainly notorious in the Fenestellidae.

An analysis of more than 17,000 measurements made on fenestellid species by the writer may be interpreted as favouring the reliability of zooecial as opposed to zoarial (i.e. meshwork) characteristics as a basis for classification. Table 1 shows the coefficients of variation ($100\sigma/m$) of 34 fenestrate forms described from the Carrick Lough residues. Examination shows that the least variable characters are inter-apertural space (representing the length of zooecial chambers) and branch width (reflecting the chamber width). The most variable ones are dissepimental width and the distance between carinal nodes, both zoarial features.

A further improvement in taxonomic practice could be effected by the utilization of accepted statistical techniques in comparing numerical data, and the rejection of the micrometric formula for the purpose. This matter has received attention elsewhere (Tavener-Smith 1966b) and will not be elaborated here. Suffice to say that in recent years fenestellid taxonomy has been beset by two major difficulties. These are, firstly, the tendency to base comparisons of fossil material on data from single fragmentary specimens; and secondly, the tendency to look for differences rather than resemblances, and to establish new species on the basis of these. In dealing with fenestrate colonies it is easy to obtain many measurements relating to meshwork features from a single fragment, but the range of these for each dimension only expresses structural variation in the fragment concerned, and has no taxonomic value. Because a single fragment cannot provide adequate data for a numerical comparison it is best, where the identity is in doubt, to refer it provisionally (cf.) to the nearest established species, and not to use it as the basis for a new one. In due course, as more material becomes available, the relationship or lack of it, should be evident and, when a number of similar specimens have accumulated, a valid numerical comparison may be made.

In the past the philosophy of classification in the Fenestellidae has been one of differences. Comparison has been effected with a view to detecting morphological differences between samples, and the erection of new species to accommodate these has led to the present situation. In a group of such morphologically diverse organisms differences are only too easy to find, and the logical end of the present procedures is a classification containing as many, or more, species than there were colonies. Use of the micrometric formula in comparing data has undoubtedly contributed to the proliferation of species, for such comparisons emphasize differences rather than resemblances, and there is no means of knowing whether the former are of taxonomic significance. The mere demonstration of some morphological difference between samples has in many cases led to the introduction of a new specific name, regardless of whether the samples or the means of comparison were adequate. In such a situation numerical methods of proved worth can render valuable assistance (Tavener-Smith 1966b). They place the comparison of data on a more objective footing, thus preventing the introduction of new species on spurious numerical grounds, while at the same time facilitating the recognition of genuine morphological differences where these exist. In the systematic descriptions that follow selected morphological statistics are arranged so that comparison with other samples may readily be effected by using orthodox biometric devices such as the t-test or the distribution of χ^2.

The following account outlines the procedure adopted in classifying fenestrate bryozoa from the Carrick Lough residues. Faunas from different collecting horizons were at first treated separately, and careful sorting led in each case to the establishment of groups of specimens with a common basic morphology. Further examination showed the presence of an almost identical range of groups in the five collections, which were, therefore, amalgamated. From each of the enlarged morphological groups a sample of between 7 and 30 (generally about 20) of the largest and best preserved fragments was selected for detailed examination. On each specimen of a sample twelve measurements were made for each of twelve variables. The mean or mode (depending on the variate) of each series was regarded as the representative datum for a specimen (Tavener-Smith 1966b : 414, 421), and from these basic measurements sample statistics were computed. These provide a quantitative statement of the morphological characteristics of a sample, and a basis for objective comparison with others of a similar nature. Where possible specimens of a sample were identified with already established species and, in such cases, the

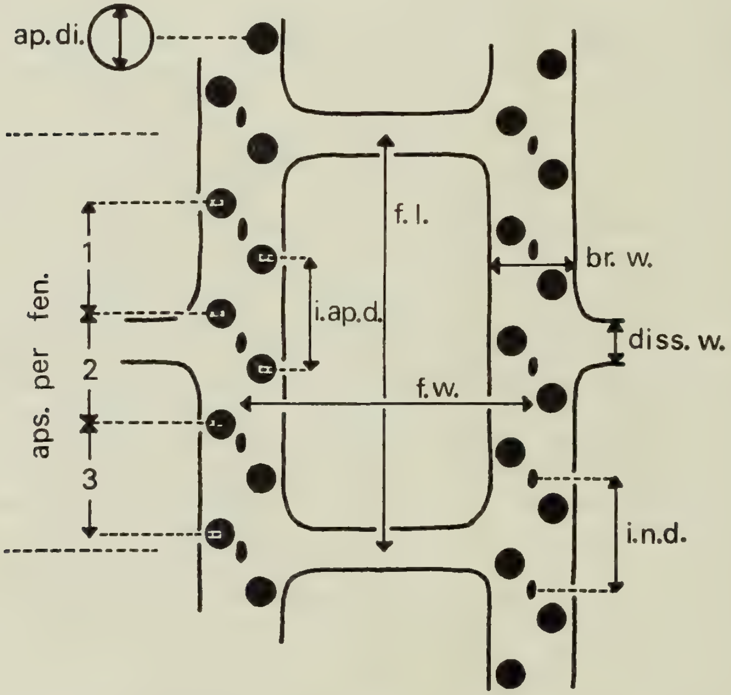

Fig. 4. Diagram showing dimensions measured for biometric purposes. ap.d., apertural diameter; aps.per fen., number of zooecial apertures per fenestrule; br.w., branch width; diss.w., dissepiment width; f.l., fenestrule length; f.w., fenestrule width; i.ap.d., interapertural distance; i.n.d., internodal distance.

sample data serve to amplify existing descriptions by furnishing a better picture of intra-specific structural variation. When different samples are compared, using a recognized biometric test, and no difference is detectable between them at the 0·05 level of significance, such samples may be considered indistinguishable for the variate concerned. In this way structurally similar groups can be amalgamated to provide larger samples, and species that were initially defined on a narrow basis may be enlarged to include other compatible groups of specimens. Eventually, as a result of this process, more natural groupings may emerge, delimited by statistically established morphological discontinuities.

The chief quantitative features considered in subsequent systematic descriptions are listed below and briefly explained. They are also illustrated in Fig. 4. Because of the nature of the fossil material, peel and thin section techniques were not applicable, and data on matters of wall structure such as the size, spacing and arrangement of skeletal rods, are therefore lacking. These data relate to characteristics of potential value in taxonomy, and it is regretted that, for the species here described, their provision must await future work.

A. Zooecial Features

1. *Inter-apertural distance:* Measured between the centres of adjacent apertures in the same row. This dimension may be treated as the equivalent of the zooecial chamber length and is a most valuable diagnostic feature.

2. *Branch width:* Measured across a branch perpendicular to its axis and away from dissepiments and branch divisions. This dimension gives an indication of the relative width of zooecial chambers, but also incorporates a variable component due to secondary skeletal growth. For this reason the coefficients of variation in branch width (Table 1) are appreciably higher than those for inter-apertural space.

3. *Apertural diameter:* Measured between the inner sides of the rim. This is essentially a zooecial feature, and it would be expected that the size would be constant for a given species, and of great taxonomic value. However, with advancing age there is an undoubted tendency for apertures to be constricted by secondary material, which seriously detracts from the usefulness of the feature. Secondary accretions may also affect the shape and rim ornament of apertures. For these reasons it is best to treat measurements of zooecial apertures with caution when comparing samples, carefully considering the age and state of preservation of the specimens.

4. *Zooecial chamber shape and size:* The chamber is a three dimensional structure and its shape is not adequately represented by base plan measurements alone. Nevertheless, in many specimens these data are the only ones available. In the descriptions that follow full accounts are given of both shape and size wherever possible, and if not, basal measurements are stated.

TABLE 1

SOME COEFFICIENTS OF VARIATION (100σ/m) CALCULATED FOR FENESTELLID SPECIES COLLECTED AT CARRICK LOUGH

	N.	Diss.w.	Ap.d.	B.w.	I.n.s.	I.ap.s.	F.w.	F.l.
Fenestella frutex	25	9·03	12·05	3·93	5·70	3·73	6·50	5·26
F. ivanovi	23	15·17	10·53	9·09	14·04	7·07	8·70	7·71
F. multispinosa	24	16·38	19·58	8·20	19·89	5·03	6·71	7·50
F. modesta	20	16·72	9·59	9·55	18·87	6·83	7·55	7·71
F. hemispherica	11	14·00	6·53	6·99	4·69	3·68	5·83	4·28
F. parallela	20	8·55	7·92	5·82	15·93	4·72	5·10	4·10
F. rudis multinodosa	22	8·88	3·93	7·26	10·88	5·00	9·04	7·58
F. plebeia	27	10·26	10·00	10·77	21·62	10·88	9·17	11·54
F. cf. *arthritica*	20	14·67	9·58	6·16	8·47	4·17	8·23	5·46
F. praemagna	16	9·46	16·27	9·83	10·56	6·48	9·87	9·46
F. fanata carrickensis	28	17·38	10·74	8·80	15·13	6·07	8·93	8·95
F. cf. *spinacristata*	25	14·69	7·27	7·20	13·53	8·02	8·59	9·27
F. cf. *funicula*	25	10·89	10·58	7·39	17·69	3·48	8·50	8·85
F. cf. *filistriata*	31	14·25	12·42	6·90	16·55	3·65	7·86	9·23
F. subspeciosa	25	13·64	7·55	7·24	14·30	4·43	7·03	8·02
F. pseudovirgosa	25	14·40	9·34	7·75	15·61	7·05	7·74	9·58
F. cf. *albida*	25	11·76	7·22	6·89	10·64	5·36	7·42	10·50
F. oblongata	20	10·25	8·33	4·62	14·28	5·84	8·51	10·74
F. delicatula	25	14·64	8·25	7·19	27·18	7·27	9·50	9·50
F. polyporata	21	10·19	5·35	5·51	12·22	3·93	5·16	11·05
F. irregularis	25	13.84	5·33	7·41	10·10	4·54	10·50	9·01
Levifenestella undecimalis	22	15·00	7·72	6·19	—	6·32	8·26	8·83
Ptilofenestella carrickensis	55	9·46	9·41	6·40	12·08	7·13	9·57	8·87
Ptiloporella varicosa	30	16·77	11·19	9·98	10·96	4·31	8·70	10·51
Minilya plummerae	10	5·89	6·90	3·91	3·42	2·50	5·21	3·31
M. nodulosa	17	10·60	9·72	11·62	7·57	5·25	7·83	7·47
M. binodata	7	10·75	11·78	2·53	2·96	1·56	3·78	2·66
M. oculata	25	13·77	9·73	3·81	4·88	3·64	8·46	6·87
Hemitrypa hibernica	30	24·41	7·66	6·26	6·71	4·61	8·48	8·74
Polypora stenostoma	15	9·87	10·88	8·16	—	6·00	8·47	8·76
P. dendroides	6	15·92	—	15·01	—	3·18	6·13	10·98
P. verrucosa	20	10·78	7·45	7·06	—	6·46	10·43	9·09
Ptylopora pluma parva	12	17·96	6·18	12·46	14·45	5·66	10·94	7·57
Septopora hibernica	10	13·59	—	5·58	—	3·00	9·51	7·14

B. Zoarial Features

1. *Fenestrule length:* Measured parallel to the growth axis between the mid-points of adjacent dissepiments. This is one of the basic dimensions of the zoarial meshwork, and also one of the least variable. The average coefficient of variation for 27 species of *Fenestella*, each represented by a sample of 20 to 25 specimens, was 8·01. Elias & Condra (1957 : 63) considered this to be the principal diagnostic character in differentiating between species of *Fenestella*.

2. *Fenestrule width:* Measured perpendicular to the growth axis and between the mid-points of adjacent branches. This is the other basic meshwork dimension. In the Carrick Lough specimens fenestrule width was slightly less variable than

fenestrule length, the coefficient of variation for the same 27 specimens previously measured being 7·75.

3. *Number of apertures per fenestrule:* Recorded as the number of *complete* inter-apertural distances in a single row between the points where the mid-lines of adjacent dissepiments meet a branch. Elias & Condra (1957 : 64) attached much importance to this feature, and to the relative positions of zooecial apertures and dissepiments. In certain species [e.g. *Fenestella tenax* Ulrich; *Minilya nodulosa* (Phillips)] the number of apertures per fenestrule and their relationship to dissepiments is regular and of obvious diagnostic value. In the majority this is not so and, because many forms have two or three apertures per fenestrule, the feature loses its usefulness.

4. *Internodal distance:* Measured between the centres of adjacent carinal nodes in the same row. Examination showed that this dimension may vary considerably within a species, and even within a single fragment. Carinal nodes are among the least regularly distributed of zoarial components, and it is, therefore, to be expected that their taxonomic value is relatively low.

5. *Dissepimental width:* Measured across the narrowest part of a dissepiment, perpendicular to its length. High coefficients of variation for this dimension (Table 1) are due to the presence of secondary accretions of varying thickness on dissepiments. The amount of secondary material is in most cases related to position within a colony. Except in a general way, such as where a form is distinguished by the uniform presence of unusually thick or thin dissepiments, this feature has little taxonomic value.

In addition to quantitative data certain other attributes may also be of value in the classification of fenestellid species. This is particularly so where features reflect, directly or indirectly, zooecial characteristics, or ones fundamental to skeletal structure such as the arrangement of skeletal rods (Tavener-Smith 1969). The three-dimensional shape of zooecia is another attribute of this kind, and so is the disposition of zooecial apertures at branch divisions where they may suggest a budding pattern. The presence of an incipient 'third row' of apertures before bifurcations, as in *Fenestella fanata carrickensis*, always merits attention, and a single aperture symmetrically placed immediately before the fork may, likewise, have taxonomic significance. The angle between newly-formed branches and the distance taken to regain parallelism, may be a function of the internal branch arrangement, and, therefore, also of diagnostic value—as, for example, in *Fenestella hemispherica* and *F.* cf. *delicatula*.

Distinctive fenestrule shapes due to the regular inflation of branch margins by zooecia may be useful in classification, particularly if associated with a symmetrical dissepiment-aperture space relationship (e.g. *Fenestella ivanovi*). Apparently diagnostic branch surface characteristics such as that mentioned above may, however, become completely obscured by secondary calcification, which militates against the taxonomic use of many seemingly valuable morphological features. Zooecial apertures and peristomial structures are very liable to alteration in this way during astogenetic development, and the same is true of the cross-sectional shape of branches or dissepiments, and the presence of longitudinal 'striae' on the reverse side.

It must be recalled (Tavener-Smith 1969) that external secondary calcification probably commenced close behind the tip of a growing branch, and that deposition continued through much of the subsequent life. Structures in the proximal regions of a colony are, therefore, commonly encrusted by secondary substance, and may differ greatly in appearance from more distally situated equivalent parts. It is completely within the realm of possibility for such differences within a colony to be of sufficient magnitude to have suggested the existence of distinct species had they occurred on separate fragments.

Secondary calcification is a constant hazard in taxonomy, and renders many apparently valuable morphological features useless. Such effects may, however, be largely excluded by the use of carefully considered quantitative attributes. For this reason reliance is placed primarily on these in the present work.

In the systematic descriptions that follow, diagnoses of species are given in the case of new taxa, and where it has been possible to assign samples with certainty to ones already established. These diagnoses are generally stated in qualitative terms, and for maximum effectiveness it is essential that they should be applied in close conjunction with the numerical data.

VI. ARRANGEMENT OF QUANTITATIVE DATA

In each of the systematic descriptions, measurements made on a stated number of zoarial fragments are given in tabular form. In taking measurements the procedure followed was that outlined in Tavener-Smith 1966b : 414, 421. The variates used are those mentioned in the preceding section and illustrated in Fig. 4. The following abbreviations are used throughout: F.l., fenestrule length; F.w., fenestrule width; I.ap.s., inter-apertural space; I.n.s., internodal space; B.w., branch width; Ap.d., apertural diameter; Diss.w., dissepiment width. Measurements are in millimetres, and the figures are arranged in four columns lettered A to D. The left-hand column (A) shows the *range of specimen mean* values within a sample. The mean for a specimen is based on twelve measurements made on that particular specimen. These specimen means are the fundamental data from which statistics given in the other columns are derived. Column B is the *sample mean*, that is, the average of the specimen means. The third column from the left (C) is the *standard deviation* of the specimen means, and the right-hand column (D) is their *coefficient of variation.*

Beneath the tabulated data, a micrometric formula is included in each of the descriptions. This is stated in the conventional manner, that is, figures are given for the number (or range) of branches and dissepiments in a space of 10 mm, and zooecial apertures and carinal nodes in 5 mm. For this purpose twelve measurements were made for each of the four variates on every specimen of a sample. In almost every case variation was encountered, and the observed range is, therefore, stated in the formula for the variate concerned.

Next, an indication is given of the number of zooecial apertures per fenestrule length. In this case also, twelve counts were made on each specimen of a sample, and the results presented in the following manner. Suppose that the number of apertures per fenestrule in a single specimen was found, in the course of making twelve measurements, to range from 3 to 5, and that the mode was 4. This is the *specimen mode.* In repeating these measurements on each of a sample of 25 specimens it might be found that the *range of specimen modes* was from 3 to 6, and that the *distribution of modes* in each of these four classes was 3, 12, 7 and 3 respectively. These data would be shown in the following way:

Apertures per fenestrule.

Range of specimen modes:	3	4	5	6
Distribution of specimen modes:	3	12	7	3

Arrangement of the data in this way facilitates comparison with other samples by means of a χ^2 test.

VII. SYSTEMATIC DESCRIPTIONS

Order CRYPTOSTOMATA Vine, 1883

Family **FENESTELLIDAE** King, 1850

Diagnosis. Zoarium a reticulate expansion of branches joined by sterile dissepiments, or by coalescence at opposed sinuous bends so as to form fenestrules; branches rarely free. Zoarium bearing zooecial apertures on one side only. Reverse smooth or longitudinally striate, and may bear small nodes.

Genus ***FENESTELLA*** Lonsdale

Fenestella Lonsdale, 1839 (nom. conserv. ICZN 1962); non Bolten, 1789.
Fenestrella D'Orbigny 1850 (non *Fenestrellina* d'Orbigny, 1850).
Actinostoma Young and Young, 1874.

Diagnosis. Zoarium funnel or fan-shaped. Zooecial openings in two rows commonly separated by a median carina bearing nodes or spines.

Discussion. The status of this generic name and the selection of a type species have been under dispute for some years. The first matter has been settled by a decision of the International Commission on Zoological Nomenclature that *Fenestella* should be a *nomen conservandum* (*Bull. Zoo. Nom.*, 1962). The type species is *Fenestella subantiqua* d'Orbigny 1850, as revised by Elias (1956; 317–324).

Fenestella, used for a group of fenestrate bryozoa, was invalid from its inception, owing to the name being already in use for a living lamellibranch (Bolten 1798). Bolten's name never became established, however, and was later placed in the synonymy of *Anomia* and, therefore, lapsed. Meanwhile d'Orbigny (1850) had used both *Fenestrella* and *Fenestrellina* in referring to the bryozoan group. The first was probably a typographical error, but the second appears to have been an attempt to rectify the irregular position affecting the name *Fenestella.* He cited *Fenestella crassa* M'Coy as the type species, Lonsdale not having designated one. The choice proved unfortunate as not only was the species not among those originally named by Lonsdale, but it was also not typical of the genus. Shrubsole concluded from an examination of topotype material that this species did not, in fact, belong to *Fenestella*, but 'to another fenestrate genus of Polyzoa' (1881 : 186). Bassler must have been unaware of this when (1935 : 110) he suspended the name *Fenestella* for bryozoans, in strict observance of the Rules of Zoological Nomenclature, and suggested that *Fenestrellina* d'Orbigny be used instead. Several authors (e.g. Crockford from 1943 onwards; Chronic 1949) adopted this usage, but by no means all. Later Bassler became aware that *Fenestrellina*, as defined by its type species, differed from *Fenestella*, and in the *Treatise on Invertebrate Paleontology, Part G—Bryozoa*, he listed the two separately. *Fenestrellina* is there defined (p. G122) as having 'Dissepiments widely separated and fenestrules very long', but being in other respects like *Fenestella*. Fortunately this ill-defined genus has been rendered invalid by Miller's (1961 : 238) discovery that the type specimen of *F. crassa* M'Coy is undoubtedly a *Polypora*. The writer has confirmed this.

When Lonsdale introduced the name *Fenestella* he included four species from the Wenlock of Dudley in the genus. They were (in the original order): *F. antiqua*, *F. milleri*, *F. prisca*, all new species, and *Retepora reticulata* Hisinger, 1837. Lonsdale's concept of a species was broader than that now acceptable, and he included in the synonymy of *F. antiqua* the earlier form *Gorgonia antiqua* Goldfuss 1829, from the Devonian of the Eifel. This name, therefore, had priority, and when it later became plain that the two were not conspecific d'Orbigny (1850) re-named Lonsdale's form *F. subantiqua*. In the same year King (1850 : 35) cited *F. antiqua* (now based on *G. antiqua* Goldfuss 1829) as the type species, a selection quite in order, but one that has given rise to some confusion, it being uncertain which of the two forms he really intended. According to Toots (1951 : 237) the type of Goldfuss' species is lost and it is impossible to recognize it from the description and figures. It therefore became necessary to adopt a new type species.

Although *F. subantiqua* d'Orbigny was not among the species originally included in the genus by Lonsdale and is, therefore, technically ineligible to be the type species, it is a reasonable choice, being almost certainly the form intended by him as *F. antiqua*. The type specimen in this case also has been lost for many years, and Shrubsole (1880 : 244), when revising the Wenlock Fenestellidae, concluded that Lonsdale's *F. antiqua* was the same as *F. plebeia* M'Coy from the Lower Carboniferous. He implied that, failing discovery of the type of *F. antiqua*, the common Carboniferous species should be treated as the type species for the genus. This seems to have prompted Ulrich's (1890 : 395) statement that *F. plebeia* is the 'accepted type' for *Fenestella*. This designation has been perpetuated in the literature (Nickles & Basler 1900 : 38; Nikiforova 1938 : 63). However, Elias (1956), working on topotype material from Dudley, succeeded in identifying Lonsdale's species and designated a neotype. This seems a satisfactory end to the matter, particularly as the form concerned fulfils the morphological requirements of *Fenestella* as at present understood. Spjeldnaes (1957 : 675) does not, however, favour the adoption of *F. subantiqua* d'Orbigny as the type species on the grounds that a doubt exists as to whether this species was named in place of *F. antiqua* Lonsdale 1839, or *Gorgonia antiqua* Goldfuss 1829. It seems most unlikely that the latter was the case, and there are much stronger arguments against the use of either *F. plebeia* M'Coy or *F. reticulata* (Hisinger) as Spjeldnaes proposed.

TYPE SPECIES. *Fenestella subantiqua* d'Orbigny 1850 (=*Fenestella antiqua* Lonsdale 1839).

Fenestella frutex M'Coy

(Pl. 1, figs 1–9)

1844 *Fenestella frutex* M'Coy; 201.
1878 *Fenestella lyelli* Dawson; 288.
1887 *Fenestella limbata* Foerste; 83.
1926 *Fenestella limbata* Foerste; Nikiforova; 175.
1929 *Fenestella lyelli* 'mut' Dawson; Bell; 101.
1934 *Fenestella* aff. *limbata* Foerste; Likharev; 155.
1937 *Fenestella limbata* Foerste; Elias; 318.
1961 *Fenestella frutex* M'Coy; Miller; 232.

DIAGNOSIS. Close-textured meshwork with branches notably thicker than dissepiments. Keels faint, with small nodes. Apertures bead-like, protruding. Zooecial chambers triangular to hemi-hexagonal.

MATERIAL. More than 70 fragments were examined, the largest being 27 × 13 mm. PD.5001–7, PD.4892–909.

Measurements made on a sample of 25 zoarial fragments (i.e. N = 25):

	A	B	C	D
F.l.	0·47–0·60	0·556	0·029	5·26
F.w.	0·40–0·52	0·461	0·030	6·50
I.ap.s.	0·19–0·21	0·201	0·008	3·73
I.n.s.	0·20–0·25	0·236	0·013	5·70
B.w.	0·22–0·27	0·254	0·010	3·93
Ap.d.	0·06–0·10	0·083	0·010	12·05
Diss.w.	0·12–0·17	0·150	0·013	9·03

Micrometric formula: 22–28/17–22//24–26/20–24.

Apertures per fenestrule.

Range of specimen modes:	2	3
Distribution of specimen modes:	23	2

DESCRIPTION. Zoarium probably a broad, roughly planar, fan-shaped expansion; branches straight and rigid in the central part, or gently curving outward towards margins of frond. Transverse section of branches sub-circular distally, becoming ovoid in the proximal parts of a zoarium due to secondary accretion. Median keel not pronounced. Branches widen progressively for three to six fenestrules prior to dividing, and may attain a width of 0·5 mm at the point of bifurcation. Immediately beyond this the width of new branches is much reduced, being commonly about 0·22 mm. Reverse side of branches well-rounded and longitudinally striated in the distal parts of zoaria. This surface may show a uniserial row of small nodes roughly coinciding with the disposition of carinal nodes on the obverse, but less regularly spaced.

Dissepiments are initially thin, broadening at either end, moderately depressed below the branch surface on both sides, and having a circular cross section. With progressing age they become encrusted by secondary growth, especially on the reverse. This leads to development of an ovoid cross section and a relatively shorter and stouter appearance.

Fenestrule shape rather variable. Distally they tend to be rectangular with rounded corners and long sides indented by one or two projecting zooecial apertures. Proximally, fenestrules are smaller (due to secondary thickening of branches and dissepiments) with elongate-oval shapes and no lateral indentations.

Zooecial apertures circular, relatively small and closely spaced. They are surrounded by plain, collar-like peristomes that are higher on the outer side. These may form inflated, cowl-like structures that partly shield apertures and project slightly into fenestrules. Prior to branch division, an incipient third row of zooecial apertures may appear for a short distance. This, with the increase of branch width in such situations, is a distinctive feature. Zooecial chambers are hemi-hexagonal (or pentagonal, see Miller 1961a : 227), in plan, though the two lateral walls may be very short, giving a near-triangular appearance. Average maximum length and width of five chambers was 0·2 mm and 0·121 mm respectively.

Carinal nodes are small and regularly placed. Distally they are circular in cross section, becoming elliptical proximally, with the long axis of the ellipse parallel to that of the branch. These elongate node-bases may unite into a long, thin, strap-like ridge raised only slightly above the branch surface. This is the only indication of a median keel. Where branches divide, carinal nodes cease immediately before the third row of apertures commences, re-appearing as soon as the new branches are established.

Short, relatively stout spines given off sparsely from obverse or reverse, and in some cases bearing recurved barbs, are a characteristic feature. They may be up to 3 mm long and 0·05 mm in diameter at the base. The length was originally greater, as all spines examined were truncated distally by breakage. Barbs are up to 0·2 mm long and sharply recurved. They may be arranged in three or four rows around the circumference of spines. Other spinose processes of comparable dimensions, but lacking barbs, occur at the lateral margins of zoarial fragments as branch continuations.

DISCUSSION. This form is *F. frutex* M'Coy, as its dimensions compare closely in all important respects with those given for the species by Miller (1961 : 232–3). The micrometric formula given by that author (on the basis of four small fragments: holotype, syntype and two homeotypes) is: 22–31/18–26//24–27/20–24. The only apparent discrepancies between the type material and that from Fermanagh relate to branch and dissepiment width. Miller's measurements of the first ranged from 0·14–0·20 mm, while in the Carrick material the range is 0·22–0·27 mm. Similarly, dissepiments were between 0·06 and 0·09 mm on the type specimens, but from 0·10 to 0·15 mm on the etched ones. It would appear that M'Coy's specimens are from the younger parts of zoaria, while those from Carrick Lough belong to the proximal region where secondary encrustation has given rise to increased dimensions. Fenestrule measurements of the Fermanagh specimens are close to those of Miller, the length varying from 0·35–0·42 mm against his 0·33–0·39 mm, and the width 0·17–0·25 mm compared with 0·22–0·33 mm. The shape of zooecial chambers and the number and arrangement of apertures in each fenestrule are identical with those described by Miller.

There is also a close structural resemblance between the present specimens and *F. fenestratum* (Young and Young) 1874, from the lower Carboniferous Limestone Series of Scotland. The generic name of that form was originally *Actinostoma*, a reference to the eight short, regularly placed apertural denticles thought to distinguish it from *Fenestella*. Later work showed, however, that this feature is also present in other fenestellid species (e.g. *Polypora radialis* Ulrich; *P. septata* Campbell) and is unlikely to be of diagnostic value at generic level. *Actinostoma* was therefore placed in the synonymy of *Fenestella* by Nickles & Bassler (1900; 37, 245).

The micrometric formula of *F. fenestratum* (calculated from ten measurements on each of six zoarial fragments) is: 19–28/19–28//19–24/17–30, with which the meshwork of the Carrick Lough specimens closely corresponds. The zooecial chamber shape is also identical in both samples, and tests of branch width and inter-apertural space failed to show a significant difference between them at the 0·01 level. In view of these important structural resemblances it is possible, not only that the Fermanagh specimens and *F. fenestratum* are conspecific but also that the latter is a junior synonym of *F. frutex* M'Coy. In view of the complete absence of apertural denticles in the Irish forms, however, it would appear premature to merge the species until the significance of this structure has been more thoroughly investigated.

Among American species the Fermanagh material most closely resembles *F. matheri* Condra & Elias 1944, from the Chester Series of Illinois. The formula for this is (Ibid : 109): 19–25/15–17//22–25/19–24, indicating the presence of larger fenestrules than in the Carrick Lough specimens. No other dimensions were given by Condra and Elias and further numerical comparison is therefore impossible. There appears, however, to be a difference in the chamber shape, that of the American species being described as (p. 110) 'rectangular, grading to pentagonal near the base'. Both forms occur at about the same stratigraphic level (*F. matheri* is from the lower Chester) but in view of the above discrepancies and the lack of further information about the American species, they cannot be regarded as conspecific.

Fenestella ivanovi Shulga-Nesterenko

(Pl. 2, figs 1–9)

1951 *Fenestella ivanovi* Shulga-Nesterenko; 100.

Diagnosis. *Fenestella* with regular, open meshwork and hour-glass shaped fenestrules. Zooecial apertures occur consistently at ends of dissepiments and mid-way along fenestrules.

Material. Thirty small fragments, the largest being 14 × 12 mm. PD.5008, PD.4682–7, PD.4910–25.

Measurements (N = 23):

	A	B	C	D
F.l.	0·45–0·60	0·515	0·040	7·71
F.w.	0·40–0·57	0·482	0·042	8·70
I.ap.s.	0·21–0·29	0·251	0·018	7·07
I.n.s.	0·21–0·37	0·265	0·037	14·04
B.w.	0·15–0·20	0·181	0·016	9·09
Ap.d.	0·05–0·09	0·171	0·008	10·53
Diss.w.	0·07–0·12	0·100	0·015	15·17

Micrometric formula: 18–23/17–22//17–25/13–26.

Apertures per fenestrule.

Range of specimen modes:	2	3
Distribution of specimen modes:	22	1

Description. Zoarium probably a small, roughly planar, fan-shaped expansion, not more than 2 or 3 cm across. The delicate meshwork of straight or gently curved branches and slender dissepiments has a characteristically regular, scalariform appearance.

Branches about as high as wide, with an approximately circular cross-section. The obverse of each branch has a poorly defined median keel, on each side of which the surface slopes gently away. Lateral branch margins are undulating owing to the projection of regularly arranged zooecial apertures into fenestrules. Reverse of branches smoothly rounded proximally, but with well-developed longitudinal striae in medial and distal parts of zoaria.

Branches are connected by regularly-placed dissepiments. These are relatively slender, and in most cases half to two-thirds of the branch width. Dissepiments are thin at the centre but wide at each end, where they unite with branches. Because the dissepimental height exceeds its minimum width, broken ends have an oval cross-section. Dissepiments are depressed below branch level on both surfaces.

Fenestrules have a characteristically hour-glass shape, due to the flaring of dissepiments at their ends and the regular indentation by zooecial apertures situated mid-way along each side. This shape is visible on both zoarial surfaces. The outline of the 'hour-glass' varies from roughly quadrate to elongate, according to the spacing of branches and dissepiments. Although this fenestrule shape is distinctive when present, it is not universally developed. A few specimens showed abnormal fenestrules with two apertures per side, only slightly undulating margins and a roughly rectangular shape.

Zooecial apertures are relatively small, round or elliptical, and placed about two diameters apart. They have low, plain, collar-like peristomes. Apertures are in most cases regularly placed: one at the end of each dissepiment and one mid-way between. In the latter situation the side of the branch is slightly inflated so that the aperture above projects into the fenestrule. Where branches divide, there is an aperture placed symmetrically in the angle of bifurcation.

Zooecial chambers have a triangular shape except where branches divide. The chamber situated in the angle may then have a diamond shape and those adjacent to it may also be irregular (commonly four or five sided) as circumstances dictate.

Average dimensions of twelve measured triangular chamber bases were: length parallel to branch axis: 0·15–0·17 mm.; maximum width: 0·12 mm.

Carinal nodes are small and commonly difficult to identify. They are uniserial and not regularly situated relative to dissepiments, though in many cases there are two nodes and rather less than two internodal spaces opposite a fenestrule. Spinose structures are present on many zoarial fragments in this species, and some examples are illustrated. Slender spines from the obverse side may be up to 3 mm long and 0·2 mm in diameter at the base. Some bear small recurved barbs distally. Long spines (up to 5 mm) also occur as sterile branch continuations. A good specimen of the proximal part of a fan-shaped colony showed a number of these that appear to have functioned as auxiliary supporting structures. In conjunction with a stout basal holdfast they maintained the colony in an upright position. It is of interest to note that the holdfast is welded onto a branch of another fenestrate meshwork, and no doubt the lateral spines were similarly attached. Bryozoan debris on the sea floor seems commonly to have provided a base from which new colonies grew.

DISCUSSION. This Fermanagh form corresponds well with Shulga-Nesterenko's (1951; 100) *F. ivanovi* from the Upper Carboniferous (C_3^{ks}) of Russia, and is assigned to that species. The micrometric formula given by that author is 18/18//18/18–21, which is within the range shown by the Irish specimens. The only apparent differences are the occurrence of slightly wider branches in the Russian form (0·2–0·25 mm against 0·15–0·2 mm) which also showed an irregular line of nodes along the mid-line of the under-surface. Specimens from Carrick Lough show no trace of the latter, but it is evident from other species that the presence or absence of such nodes has little diagnostic importance. More interesting is Shulga-Nesterenko's statement that peristomes in *F. ivanovi* are petaloid, a feature that she also illustrated (1951; 101, fig. 38). Her thin section (Ibid., pl. XIX, fig. 1) shows that the petaloid shape, which may be equated with the 'marginal denticles' of *F. fenestratum* and other species, does not persist below the aperture. Furthermore, the fact that the petaloid shape was associated by Shulga-Nesterenko with the peristome, a secondary structure, could be taken as an indication that such apertural shapes are old-age characteristics. The slightly greater branch width of the Russian specimens as compared with those from Fermanagh would then also be readily explained.

The regular, scalariform meshwork of the Carrick Lough specimens, together with their hour-glass fenestrules, are reminiscent of Foerste's (1887, pl. VII, figs 10a–d) illustration of *F. limbatus*. Unfortunately Foerste's description is vague and lacks quantitative data, so that it fails to provide a basis for comparison. Shulga-Nesterenko (1951; 79) also recorded the species, however, and included many measurements in her description. She differentiated Foerste's form from *F. ivanovi* chiefly on the basis of meshwork dimensions and zooecial chamber shape. With a formula of: 25/23//25–26/25, her *F. limbatus* had a finer textured meshwork; it also had hemi-hexagonal zooecial chamber bases. Dimensions of the specimens from Carrick Lough are closer to *F. ivanovi* than *F. limbatus* and, like the former, have triangular chamber bases.

Fenestella multispinosa Ulrich

(Pl. 3, figs 1–9)

1890 *Fenestella multispinosa* Ulrich; 540.
1906 *Fenestella multispinosa* Ulrich; Cumings; 1278.
1926 *Fenestella multispinosa* Ulrich; Nekhoroshev; 1245.
1926 *Fenestella multispinosa* Ulrich; Nikiforova; 178.
1927 *Fenestella multispinosa* var. *karakubensis* Nikiforova; 247.
1933 *Fenestella multispinosa* Ulrich; Nikiforova; 16.
1942 *Fenestella multispinosa* Ulrich; Kaisin; 93.
1942 *Fenestrellina multispinosa* (Ulrich); McFarlan; 444.
1944 *Fenestella multispinosa* Ulrich; Condra and Elias; 110.
1948 *Fenestella multispinosa* Ulrich; Nekhoroshev; 24.
1951 *Fenestella multispinosa* Ulrich; Shulga-Nesterenko; 85.
1962 *Fenestella multispinosa* Ulrich; Miller; 121.

DIAGNOSIS. Colonial meshwork similar to *F. frutex* but slightly coarser and with zooecial apertures protruding less. Branch obverse more flattened, with good median ridge bearing slender nodes.

MATERIAL. This is a common form in the Carrick Lough residues. Seventy-four zoarial fragments were examined, the largest being 29 × 18 mm. PD.4688–94, PD.4926–41.

Measurements (N = 23):

	A	B	C	D
F.l.	0·55–0·72	0·633	0·047	7·50
F.w.	0·45–0·57	0·499	0·033	6·71
I.ap.s.	0·22–0·30	0·250	0·012	5·03
I.n.s.	0·27–0·55	0·358	0·071	19·89
B.w.	0·22–0·30	0·250	0·021	8·20
Ap.d.	0·07–0·12	0·096	0·019	19·58
Diss.w.	0·10–0·17	0·016	0·019	16·38

Micrometric formula: 19–23/13–18//18–23/9–18.

Apertures per fenestrule.

Range of specimen modes:	1	2	3
Distribution of specimen modes:	1	22	1

DESCRIPTION. Zoarial shape uncertain from the fragments examined. It may have been a fan-shaped expansion of moderate size (several cm across) or a foliaceous meshwork arising from a cup-shaped growth origin.

Branches straight or gently curving; strong and presenting a rigid appearance. A low median ridge on the obverse follows the branch axis and on each side of this the surface slopes sharply away. The reverse also may bear a poorly defined median keel, though proximally this is obscured by secondary material and the surface tends to be broadly rounded. Where a median ridge is present on both sides the branch has a diamond-shaped cross section, otherwise it tends to be angular above and rounded below. Faint longitudinal striae are commonly present on the reverse. Before a branch divides its width increases progressively for a distance of two to four fenestrules, and at the point of bifurcation the normal width of about 0·25 mm may be doubled. Beyond this new branches are narrower than usual, a width of about 0·17 mm being common. On the reverse of a few specimens there were localized secondary encrustations of unusual thickness. These caused considerable increases in branch width, in some cases to as much as 0·77 mm. The thickenings were particularly evident at branch divisions and also affected adjacent dissepiments.

Dissepiments are slightly depressed below branch level on both sides of the meshwork. They are more slender than branches and thinnest in the middle, increasing in width at either end. Where the reverse of a branch is angular (i.e. has a median ridge) that of adjacent dissepiments may be similar, though the obverse of dissepiments is invariably rounded. Due to the tendency for dissepiments to flare at their ends, fenestrules have rounded extremities. Fenestrule shapes are most commonly rectangular or quadrate, though they may be elongate-oval or elliptical in older parts of zoaria. Fenestrule margins may be gently sinuous owing to the tendency for zooecial apertures to project slightly.

Apertures are circular and commonly have low, plain, ring-like peristomes. Zooecial chambers are hemi-hexagonal in plan. The average dimensions of eleven measured chambers were: maximum length parallel to growth axis: 0·275 mm; maximum width: 0·137 mm; width of short lateral walls: 0·075 mm.

Carinal nodes, where well preserved, are slender and up to 0·15 mm high. In most cases they are broken or abraded off and difficult to locate. The spacing of nodes varies considerably between fragments and is unlikely to be of diagnostic value. The reverse of a few specimens bears an ill-defined row of unevenly distributed nodes along the mid-line. These vary in diameter from 0·02 to 0·07 mm. Spinose structures up to 5 mm long are present on some zoarial fragments. They originate from the reverse side or laterally, as branch continuations, and may bear recurved barbs at their distal ends.

Discussion. Zooecial apertures in this species varied considerably in diameter and this is reflected in a high coefficient of variation. The differences appear to be due partly to imperfect replacement of original structures by silica. They may also to some extent be attributed to age differences, as apertures appear to have been progressively constricted by secondary calcareous deposits. Thus the size of zooecial apertures on a fragment tends to be related to its original position in the zoarium.

Some specimens showed evidence of the remarkable capacity of fenestrate colonies to regenerate after sustaining structural damage. One rectangular fragment 22 × 5 mm appears to have broken from the parent colony at the proximal end and laterally. Evidence of recovery includes the sealing of broken branch ends by copious deposits of secondary material. Two broken branches subsequently continued their growth but in the *opposite direction*, in other words, towards the growth origin. One of them divided in the ordinary way but at 180° to the normal direction. A number of stout trabeculae grew from the damaged ends of adjacent dissepiments to support these aberrant branches.

Another specimen provides an even more striking example of recovery from breakage which, in this case, caused part of the meshwork to diverge from the rest by about 30°, though still attached proximally. Recovery involved (a) sealing of broken ends of dissepiments by secondary deposits; (b) the development from others of strengthening struts to hold the broken section in a rigid and stable position; (c) renewal of growth in a *reverse* direction from the broken ends of some branches, including the bifurcation of these in the same direction; and (d) renewal of growth in a normal, forward direction from the broken ends of other branches. Breakage appears to have acted as a growth stimulant in this case. The value of copious secretion of secondary material in effecting structural repairs is very evident.

Comparison with established species shows that Fermanagh specimens of this kind are close to Ulrich's (1890 : 540) *Fenestella multispinosa*. The micrometric formula of that species, based on Ulrich's description, is: 20–21/14–15//21/?. He made no mention of carinal nodes but it appears probable from his illustrations that the number was between 18 and 23 per 5 mm. Fewer nodes have been counted on specimens assigned by other authors to this species, e.g. 'about 18' (Condra & Elias 1944 : 112), 12–15 (Nikiforova 1927 : 246) and 'about 14' (Nekhoroshev 1926 : 1245). The Carrick material corresponds closely in node counts and in other dimensions with the last description. Nekhoroshev's illustration (Ibid., pl. XX, fig. 3) shows hemi-hexagonal to triangular base shapes similar to those of the Irish specimens. There are discrepancies in the literature regarding this feature, however. Ulrich's description (1890 : 540–541) does not mention chamber shape, but one of his illustrations (Ibid., pl. L, fig. 3d) shows it to be rectangular or just hemi-hexagonal. Condra and Elias (1944 : 112) state that the chamber shape is rectangular, as does Miller (1962 : 122). Shulga-Nesterenko (1951, pl. XVI, fig. 2) shows it as hemi-hexagonal to triangular, mainly the latter. The illustration of *F. multispinosa* var *karakubensis* Nikiforova (1927, pl. XII, fig. 3) may, however, explain these differences. It shows quite clearly and within the same fragment, chambers that vary in plan from near rectangular, through hemi-hexagonal to sharply triangular. The variations do not seem to be due to sectioning at different levels, but may bear a relationship to branch width, as the shapes are more rectangular in wide branches and triangular in narrow ones.

The Carrick Lough specimens also show resemblances to Ulrich's (1890) *F. sevillensis* which has the formula: 20/16//16–17/?. An important difference between the two appears to be the wider spacing of zooecial apertures in the American form. Ulrich gave no other useful structural information and, because the species has not been described elsewhere, further comparison is impossible.

Fenestella modesta Ulrich

(Pl. 4, figs 1–6)

1890 *Fenestella modesta* Ulrich; 550.
1929 *Fenestella modesta* Ulrich; Moore; 21.
1962 *Fenestella* cf. *modesta* Ulrich; Miller; 124.

Diagnosis. Thin branches and dissepiments enclose relatively large rectangular fenestrules. Good median keels. Apertures small, widely spaced, three per fenestrule. Protruding peristomes may give branch margins a sinuous aspect.

Material. This is not a common form in the residues. Only 40 small fragments were available, the largest measuring 13 × 8 mm. PD.4695–8, PD.4942–57.

Measurements (N = 20):

	A	B	C	D
F.l.	0·65–0·92	0·804	0·062	7·71
F.w.	0·50–0·65	0·572	0·043	7·55
I.ap.s.	0·22–0·29	0·260	0·018	6·83
I.n.s.	0·22–0·40	0·305	0·057	18·87
B.w.	0·17–0·22	0·204	0·190	9·55
Ap.d.	0·07–0·09	0·073	0·070	9·59
Diss.w.	0·09–0·15	0·126	0·021	16·72

Micrometric formula: 15–20/11–15//18–22/12–20

Apertures per fenestrule.

Range of specimen modes:	2	3	4
Distribution of specimen modes:	6	13	1

Description. Zoarial fragments have an open-textured meshwork of intermediate size, consisting of relatively thin branches and dissepiments with rectangular fenestrules. Specimens are mostly small, giving no certain indication of zoarial shape, though it is probable that this was of the orthodox planar, fan-shaped kind.

Branches are slender in relation to fenestrule size; they are straight and mostly parallel, except in the proximal region where they bifurcate repeatedly and tend to curve outward. There is a median keel on the obverse. This is clearly marked in distally located fragments but tends to be obscured by secondary encrustation in ones from the proximal part of a colony. In younger fragments the upper surface of a branch slopes sharply away on either side of the keel; more gently in older ones. The margins of branches are in most cases gently sinuous owing to the presence of a slight bulge below each aperture. This is particularly evident on the reverse. The under surface of branches is broadly rounded and commonly shows good longitudinal striae. These may also be visible on the flanks of branches between apertures.

Dissepiments are bar-like, with roughly circular section and do not expand much at the ends. They are slender in the distal region, but shorter and stouter in older, more encrusted parts of colonies. Dissepiments are considerably depressed below the branch crest on the obverse side, but only slightly on the reverse. They bear striations parallel to their length, and on the under side these are continuous with similar markings on adjacent branches.

Fenestrules are comparatively large, commonly 1½ to 3 times the branch width. In most cases they are rectangular with slightly sinuous lateral margins; less commonly they may be almost quadrate (where branches are widely spaced) or elongate-oval to elliptical.

Zooecial apertures small, circular and relatively widely spaced (about 1½ to 3 diameters apart). Although they show a tendency to regular occurrence in relation to dissepiments, with one opposite the end of each, this is by no means general and they are not 'stabilized' in the sense of Elias & Condra (1957 : 70). Apertures are situated on the sloping obverse surface of branches and are directed obliquely 'upward'. Some fragments have branches with a laterally compressed appearance, and in these zooecial apertures may face more or less directly into fenestrules. Plain, collar-like peristomes are commonly present. In some cases the lower margin of the peristome is extended and may project into the fenestrule as a hood, partly obscuring the aperture. The appearance is then reminiscent of the lunaria of *Fistulipora* and related genera.

Zooecial chambers are triangular or trapezoid in plan. Average measurements of four triangular chamber bases were as follows. Length parallel to branch axis: 0·17 mm; maximum width: 0·1 mm. Trapezoid chamber bases have slightly larger dimensions (length of longest side: 0·19 mm; length of shortest side: 0·03 mm; width: 0·13 mm).

Carinal nodes are not prominent in this species, the only sign of their former presence commonly being elongate spine bases on the obverse mid-line of branches. Where nodes are preserved they are slender and up to 0·12 mm high. Long spinose structures that are the sterile continuations of branches are present on some zoarial fragments. One of these was 1·77 mm long and had a basal diameter of 0·22 mm. The distal end, truncated by breakage, was 0·17 mm across. Another spine with the same basal diameter was 4·25 mm long, and a third, 2·5 mm long, was expanded at the distal end and attached to another fenestrate colony. These spines, directed laterally from the zoarial margin, appear to have been supporting structures that helped to maintain the colony in its growth position. Other spines, originating from the obverse and reverse of the meshwork, are fewer and less strongly developed than the lateral ones.

Some branches bear a row of small, closely spaced nodes along the mid-line on the reverse side. These are about 0·02 mm in diameter and are spaced one or two diameters apart. Other nodes may be similarly distributed on the under side of dissepiments. One small specimen bore so many strongly developed and closely spaced spines and nodes that it probably represents a pathological condition. The carinal spines are taller and closer than is usual, and several that are particularly well developed branch at their summits, giving rise to clumps of spreading processes resembling the antlers of a deer. Other spines sprout from the flanks of branches above, below and between zooecial apertures. There are also prominent nodes along the reverse mid-line.

Discussion. Specimens of this form compare in all respects with Ulrich's description of *F. modesta* and are assigned to that species. Miller (1962 : 124) tentatively assigned a specimen from the Lower Carboniferous Limestone Series at Dalry, Ayrshire, to the same species. It showed most of the features of the American form but had smaller fenestrules which Miller, quite reasonably, attributed to excessive secondary encrustation. Nevertheless, an important discrepancy remains, for his specimen had notably larger zooecial apertures than those observed by Ulrich. Zooecial apertures on the Fermanagh specimens correspond more closely in size and spacing with Ulrich's description.

In the opinion of the writer this form is undoubtedly the *Retepora tenuifila* described and illustrated by Phillips (1836 : 199 and pl. 1, figs 23–25) from the

Carboniferous Limestone at Florence Court, Fermanagh, about fifteen miles from Carrick Lough. The horizon from which Phillips obtained his material was almost certainly in the D_1 subzone and roughly equivalent to that of the writer's collecting locality. Although Phillips' description is quite inadequate by modern standards, as far as it goes the specimens discussed here respond to it in every particular. His fig. 23 shows the slim, straight branches and dissepiments, and relatively large rectangular fenestrules. This diagram is drawn to natural size, with which the Carrick Lough specimens agree. Fig. 24 illustrates the striated nature of the under side of branches, and 25 shows the gently undulating fenestrule margin with the same number of small, rather widely spaced zooecial apertures as in my specimens. This figure also indicates the keeled nature of the branches, and the fact that they are commonly wider than dissepiments. Phillips' (1836 : 199) use of the phrase, 'pores small, with prominent edges' presumably refers to the collar-like peristomes surmounting zooecial apertures, and also present in the Carrick material. Elias (MS. 1950 : 1) identified specimens in the Hunterian Museum, Glasgow University as '*Fenestella tenuifila* Phillips', and gave the micrometric formula: 18–20/11·5–18//17–20/16. The present specimens agree well with this. He also recorded the number of apertures per fenestrule as 2·4 to 4, mostly 3, and the shape of the zooecial chamber as trapezoid, as in the Fermanagh material.

These similarities, taken in conjunction with the stratigraphic equivalence and proximity of the collecting localities, make it seem almost certain that the two forms are conspecific. Nevertheless, the Carrick Lough specimens cannot be assigned to *F. tenuifila* (Phillips) 1836, for the type material of that species is believed lost. For that reason Miller (1961 : 225) declared the name a *nomen dubium* and the Carrick Lough material is, therefore, assigned to Ulrich's species.

Fenestella hemispherica M'Coy

(Pl. 4, figs 7–9; Pl. 5, figs 1–4)

1844 *Fenestella hemispherica* M'Coy; 202.
1881 *Fenestella hemispherica* M'Coy; Shrubsole; 181.
1961 *Fenestella hemispherica* M'Coy; Miller; 229.

DIAGNOSIS. A framework of strong, parallel branches joined by short, narrow dissepiments encloses elongate-rectangular fenestrules. A prominent median keel supports regularly spaced nodes. Zooecial chambers hemi-hexagonal.

MATERIAL. This form is scarce in the etched residues. Only 17 fragments were examined, the largest measuring 18 × 10 mm. PD.4699–704, PD.4958–62.

Measurements (N = 11):

	A	B	C	D
F.l.	0·75–0·87	0·823	0·035	4·28
F.w.	0·47–0·57	0·532	0·310	5·83
I.ap.s.	0·24–0·26	0·251	0·009	3·68
I.n.s.	0·52–0·60	0·559	0·026	4·69
B.w.	0·22–0·27	0·243	0·017	6·99
Ap.d.	0·10–0·12	0·115	0·007	6·53
Diss.w.	0·07–0·12	0·100	0·014	14·00

Micrometric formula: 18–22/11–13//18–20/8–9.

Apertures per fenestrule.

Range of specimen modes:	2	3	4
Distribution of specimen modes:	2	8	1

Description. The small fragments available for study, though well preserved, give no indication of the zoarial shape. All belonged to the intermediate parts of colonies and are roughly planar, with parallel branches. They could have come from the medial region of large, fan-shaped meshworks, but it is more likely that they formed parts of cone- or funnel-shaped zoaria of the kind illustrated by M'Coy (1844 pl. XXIX, fig. 4a).

Branches are straight, parallel and of moderate width. For two to four fenestrules before a branch divides its width gradually increases, and may reach 0·47 mm at the point of bifurcation. Immediately afterwards this reduces to about 0·2 mm in the new branches. A longitudinal median keel is present on the obverse and in younger fragments the branch surface slopes steeply away from this. On older ones, and approaching branch junctions, the slope is less pronounced and upper surfaces of branches may be almost smoothly convex. The under side is broadly rounded and longitudinally striated.

Dissepiments are characteristically short, thin and depressed below the branch surface on both sides. They have a roughly circular cross-section and, due to secondary accretion, may be comparatively stout in older zoarial fragments. Dissepiments increase sharply in width at their ends.

Fenestrules are commonly elongate-rectangular, with the length varying from 1½ to 3 times the width. Lateral margins are straight, as zooecial apertures do not project from branches. In most cases fenestrules are as wide, or a little wider than branches; rarely they may be 1½ times the branch width.

Zooecial apertures are circular and from 1 to 1½ diameters apart. There may be thin, low, rim-like peristomes, but these do not project into fenestrules. At branch divisions an aperture is commonly placed symmetrically in the angle of divergence, but this is by no means always so, and in some specimens the disposition of apertures in this situation is slightly irregular. Zooecial chambers have a hemi-hexagonal base shape and the average measurements of six were: length, 0·25 mm; and width, 0·137 mm.

Carinal nodes are small and regularly placed, though relatively widely separated. They are slender, inconspicuous except in profile view, and up to 0·14 mm high (about half as high as a branch). A characteristic feature seems to be the presence of low, rounded nodes along the mid-line on the under side of branches. These may be situated opposite branch-dissepiment junctions, but not always. They are smooth, rounded swellings up to 0·08 mm high and 0·05 to 0·1 mm in diameter. In one specimen slit-like holes up to 0·1 mm long and parallel with the branch axis were seen on the sites of nodes that had been removed by breakage or abrasion. Such openings, piercing encrustations of secondary material, denote (like those seen in carinal nodes) the former presence of the primary skeleton. It is, therefore, probable that these nodes are primary structures and not just excrescences associated with secondary encrustation.

Discussion. This form agrees perfectly with M'Coy's (1844 : 202) description of *Fenestella hemispherica* from the Irish Lower Carboniferous, and the fragment he illustrated (pl. XXIX, fig. 4b) could well be one of the writer's specimens. With the text of Miller's (1961 : 229) description there is also close agreement, though the micrometric formula given by that author (20–27/12–15//20–21/10–12) indicates that in his material branches and carinal nodes were slightly more closely spaced than in the specimens from Carrick Lough. Miller's formula was based on only two small fragments however, and they were from a different locality and horizon (top Tournaisean or low Visean). In these circumstances it seems reasonable to attribute the differences to intra-specific variation, and the writer has no hesitation in assigning the specimens described here to M'Coy's species. Because the literature contains hardly any references to *Fenestella hemispherica*, and in view of the scarcity of fragments of this kind in the etched residue, it must be concluded that the species is uncommon.

Fenestella parallela Hall

(Pl. 5, figs 5–9)

1881 *Fenestella parallela* Hall; 26.
1887 *Fenestella parallela* Hall; Hall and Simpson; 107.
1958 *Fenestella parallela* Hall; Koenig; 138.

Diagnosis. Similar meshwork to *F. hemispherica*, from which it differs in having broader branches and fenestrules, more widely spaced apertures and more closely spaced carinal nodes.

Material. This form is moderately common and more than 50 fragments were examined. They were mostly quite small but one, from the medial part of a colony, measured 45 × 22 mm. PD.4705–11, PD.4963–75.

Measurements (N = 20):

	A	B	C	D
F.l.	0·75–0·87	0·829	0·034	4·10
F.w.	0·52–0·65	0·600	0·030	5·10
I.ap.s.	0·25–0·30	0·270	0·013	4·72
I.n.s.	0·27–0·05	0·390	0·062	15·93
B.w.	0·25–0·32	0·287	0·017	5·82
Ap.d.	0·10–0·12	0·110	0·009	7·92
Diss.w.	0·12–0·17	0·146	0·012	8·55

Micrometric formula: 16–23/11–13//17–20/10–18.

Apertures per fenestrule.

Range of specimen modes:	2	3
Distribution of specimen modes:	3	17

Description. Fragmentary specimens examined give no certain indication of the zoarial shape. This could have been a slightly undulose, fan-shaped expansion, or an elongate cone. Colonies must have attained a considerable size, for the largest fragment available was from the medial region and showed no sign of proximal or distal parts.

Branches are relatively stout, straight and more or less parallel (suggesting that the fragments are from the medial or distal parts of colonies). There is a feebly developed median ridge on the obverse, and the branch surface slopes gently away on each side of this. The reverse is broadly rounded and faintly striated, though the striae may be obscured by a coating of secondary schlerenchyma. Branches widen progressively for two to four fenestrule lengths before dividing, and may attain a width of 0·62 mm at the point of division. At the same time the obverse becomes almost flat. Immediately after bifurcation branch width is reduced to about 0·27 mm.

Dissepiments are short, bar-like and depressed only slightly (if at all) below branch level on both sides. The width increases considerably at either end approaching the union with a branch. Coarse ridges and grooves commonly traverse dissepiments along their length and unite with corresponding features on the flanks and under side of branches. Broken ends of dissepiments have a roughly circular cross section, though it may be elliptical in older fragments due to preferential deposition of secondary material on upper and lower surfaces.

Fenestrules are rectangular with rounded extremities, and commonly about 1½ to 3 times as long as they are wide. The width is in most cases slightly greater than that of branches, and lateral margins may be straight or slightly indented by zooecial apertures. The latter are circular and spaced about one diameter apart. They may have plain, circular, rim-like peristomes, though these are not strongly developed. Where a branch widens prior to bifurcation the arrangement of zooecial apertures may be slightly irregular. A few specimens showed a short 'third row' of about two apertures in this position. Zooecial chambers are hemi-hexagonal in base plan. Seven were measured and the average dimensions found to be: maximum length, 0·3 mm; maximum width, 0·12 mm.

Carinal nodes are small, poorly developed and commonly difficult to identify. Their spacing along the median ridge varies from one specimen to another. Nodes are cylindrical in the distal parts, but proximally are compressed from side to side. The elongate-elliptical node bases are 0·07–0·1 mm long and parallel with the branch axis. A few specimens had strong spinose structures growing from the reverse side. These were up to 9 mm long with a proximal diameter of 0·4 mm. Some bore recurved barbs up to 0·12 mm long at their distal ends.

Discussion. The presence of long, barbed spines growing from the under surface of branches suggests that the zoarial shape was planar rather than infundibular. Most funnel-shaped colonies of *Fenestella* have the zooecial apertures on the outer surface (Cumings 1904 : 72), and that being so, long spines from the reverse would have grown into the funnel. It is difficult to visualize any useful purpose for such an arrangement. With a planar meshwork lying on the sea floor, on the other hand, hooked spines from the under side could have acted as anchors in much the same fashion as the grapnel radicles in species of present day *Scrupocellaria* (Hinks 1880 : pl. 7, fig. 6). However, most forms of *Fenestella* do not seem to have had a prostrate growth habit, and certainly some specimens bearing barbed appendages had an upright or partly upright posture (e.g. Elias & Condra 1957 : pl. 17, fig. 4).

Also, barbed spines are not restricted in occurrence to the reverse side of meshworks but in some species grow from the obverse, or arise laterally as branch continuations. It seems likely that in many cases these spines fulfilled their apparent purpose of helping to stabilize colonial meshworks by engaging with other organisms that lay or grew on the sea floor.

Superficial morphological resemblances and similar micrometric formulae (differing only in the number of carinal nodes), at first suggested that these specimens were conspecific with the ones assigned to *F. hemispherica.* Closer examination and the use of t-tests indicated other important discrepancies, however. Statistically significant differences ($P < 0{\cdot}05$) between the samples were found to be present in fenestrule, branch and dissepiment width, and also in the spacing of zooecial apertures. As the *F. hemispherica* sample had both thinner branches and narrower fenestrules, these differences could not be attributed to secondary encrustation. In view of this and the lack of correspondence in the spacing of zooecial apertures (hence also in the length of zooecial chambers) it was concluded that the samples were not conspecific.

Comparison with described species of *Fenestella* showed that the specimens under discussion coincide in all respects with *F. parallela* Hall 1881, as recorded from the Chouteau Group (Kinderhookian) of Missouri by Koenig (1958 : 138–140). The micrometric formula given by that author is: 15–21/12–19//16–18/12–18. This is within the range of variation shown by the Carrick Lough specimens, which also show close agreement with other dimensions given by Koenig. There is a minor difference in fenestrule length; that of the Chouteau form being 0·55 mm as against an average of 0·6 mm in specimens collected by the writer. It is interesting to note that Koenig (p. 138) gave the zoarial shape as, 'a flabellate expansion', whereas Hall & Simpson (1887 : 107) stated that it was infundibular. Their illustrations (particularly pl. XLIV, figs 8 and 9) do not support this statement, however. Hall (1881 : 24) originally recorded the species from the Middle Devonian of New York, Ohio and Alabama, and Koenig's material came from the lower and middle Chouteau, and is probably of Tournaisian age. The Carrick Lough material, therefore, appears to represent a late survival of the species, and extends its range into the Visean.

Although the writer feels in no doubt that these specimens should be assigned to Hall's species, the possibility that *F. parallela* and *F. hemispherica* are closely related and perhaps even conspecific should be borne in mind. The question may be resolved as more material becomes available.

Fenestella rudis Ulrich ***multinodosa*** subsp. nov.

(Pl. 6, figs 1–7)

MATERIAL. A moderately common form of which 47 zoarial fragments were studied. The largest measured 20 × 8 mm. PD.4712–16, PD.4976–92.

Measurements (N = 22):

	A	B	C	D
F.l.	0·75–1·07	0·917	0·070	7·58
F.w.	0·52–0·82	0·652	0·059	9·04
I.ap.s.	0·25–0·31	0·275	0·014	5·00
I.n.s.	0·20–0·30	0·255	0·028	10·88
B.w.	0·30–0·40	0·334	0·024	7·26
Ap.d.	0·12–0·13	0·127	0·005	3·93
Diss.w.	0·17–0·25	0·231	0·020	8·88

Micrometric formula: 14–19/9–13//15–20/18–25.

Apertures per fenestrule.

Range of specimen modes:	2	3
Distribution of specimen modes:	1	21

Diagnosis. These specimens have the typical *F. rudis* meshwork of stout, transversely flattened branches with wide dissepiments and elongate-oval fenestrules. Prominent zooecial apertures are closely spaced, commonly with three per fenestrule. Inconspicuous carinal nodes surmount the median ridge. Though small, these are numerous and distinguish this form from *F. rudis* s.s. Zooecial chamber plan hemi-hexagonal or triangular.

Type specimens. Holotype: PD.4712, Paratypes: Other zoarial fragments numbered PD.4713 to PD.4716.

Description. The specimens appear to have formed parts of zoaria of moderate size (say 3 to 6 cm across), with the form of planar or gently undulating, fan-shaped expansions. The near-parallelism of branches and lack of bifurcation suggests that most of the fragments were from the medial or distal parts of colonies.

Branches are relatively broad, stout and straight. They are rather flat on the obverse, where there is a low but clearly defined median ridge. On each side of this the surface slopes gently away to the fenestrules. In plan the margins of branches show a shallow concave curve between adjacent dissepiments. The reverse is broadly rounded or sub-angular. Branch width increases greatly at bifurcations and may reach 0·85 mm, reducing immediately beyond to about 0·28 mm in each new branch.

Dissepiments are short and stout, thinnest in the middle and rapidly increasing in width at either end. They are regularly placed and may be striated parallel to the length. Dissepiments are notably depressed below branch level on the obverse but only slightly, if at all, on the reverse. On that side secondary encrustation may cause dissepiments to be flush with a branch or even to project a little below it.

Fenestrule shapes are mostly elongate-oval or rectangular with rounded extremities, the latter due to the shape of dissepiments. In most cases the length of fenestrules is about one-and-a-half-times, or twice the width.

Zooecial apertures are relatively large, closely spaced (about one diameter apart) and in two alternating rows placed well out towards branch margins and away from the median ridge. Apertures face obliquely upward and outward. They have only feebly developed peristomial rims and do not, as a rule, project into fenestrules. At branch divisions an aperture may be symmetrically placed in the angle of divergence. Zooecial chamber bases are hemi-hexagonal or triangular. In the first case the lateral walls are well developed, and in complete chambers are seen to be inclined distally at about 50°. Average dimensions of eight measured chambers were: length parallel to branch, 0·2 mm; maximum width, 0·21 mm; length of lateral walls (perpendicular to branch axis), 0·09 mm. Four triangular chambers gave the following average measurements: length parallel to branch, 0·27 mm; maximum width, 0·19 mm.

Carinal nodes are small, and in many cases only identifiable from the position of elliptical basal scars. The spacing varies even within a single zoarial fragment. Node base scars may be pierced by elongate slits, and in a few cases these unite to form a narrow, thread-like cavity along the mid-line of a branch. Such cavities indicate the former presence of the primary skeleton. The arrangement of carinal nodes on many branches is somewhat irregular and not perfectly uniserial.

One or two specimens showed unusually heavy localized encrustations of secondary schlerenchyma on fragments from the medial parts of zoaria. The thickening affected both surfaces, and on the obverse a number of zooecial apertures were occluded and the tips of carinal nodes only distinguishable as fine perforations. On the same side were the truncated stumps of a number of stout, proximally-inclined spines. The maximum length of these was only 1·5 mm but basal diameters were up to 0·5 mm.

Discussion. In matters of zoarial size, shape and most meshwork characteristics this form corresponds with Ulrich's *Fenestella rudis* from the Keokuk and Warsaw formations (probably late Tournaisean to mid-Visean) of the United States. It is said, however, (1890; 537) that dissepiments in that species are 'comparatively weak, rarely half as wide as the branches'. Those of the Carrick Lough specimens are stouter than this, but otherwise of similar character. Dissepimental width is, in any event, a notably variable feature. A more important discrepancy relates to the distribution of carinal nodes, Ulrich's material showing only between nine and thirteen of these per 5 mm Elias (1964; 378) reduced this range to 10–12 in his emended description of the species. Although the spacing of nodes is also known to show considerable intra-specific variation, the differences involved here are too marked for the Carrick specimens to be included with *F. rudis* ss. Nikiforova (1926; 178) described a variant, *F. rudis major*, from the Lower Carboniferous of Turkestan. This had fifteen nodes per 5 mm but in all other respects compared closely with the present material. The difference in internodal space (given by Nikiforova as 0·325 mm) is still too great to allow the two forms to be considered identical, however, and it seemed wisest in the circumstances to introduce a new subspecific name for the etched specimens.

In his recent paper, Elias (1964; 378–379) erected two new species, using specimens originally included by Ulrich (1890) in *F. rudis*. These were *F. iowensis* and *F. rudiformis*, and the formulae of the three stated by Elias, are as follows:

F. rudis s.s.	16–18/12·5–13·5//18–21/10–12
F. iowensis	14–17/11–14//18–20/12
F. rudiformis	15–20/10·5–14·5//18–20/10–12

The species were differentiated solely on minor variations of fenestrule length and zoarial shape. It is difficult to see any reason for the introduction of new names here, as the variations in question are of exactly the type and magnitude that would be expected to occur within a single species.

Fenestella plebeia M'Coy

(Pl. 7, figs 1–7)

1844 *Fenestella plebeia* M'Coy: 203.
1844 *Fenestella ejuncida* M'Coy: 201.
1850 *Fenestella plebeia* M'Coy; d'Orbigny: 152.
1879 *Fenestella plebeia* M'Coy; Shrubsole: 278.
1881 *Fenestella plebeia* M'Coy; Shrubsole: 179.
1895 *Fenestella plebeia* M'Coy; Stuckenberg: 138.
1933b *Fenestella plebeja* M'Coy; Nikiforova: 10.
1934 *Fenestella plebeja* M'Coy; Prantl: 4.
1948 *Fenestella* aff. *plebeia* M'Coy; Oakley: 89.
1961 *Fenestella plebeia* M'Coy; Miller: 226.

DIAGNOSIS. *Fenestella* with medium-textured meshwork of sub-parallel, straight-sided branches bearing strong median keels and closely spaced carinal nodes. Apertures laterally directed, usually four along the side of each elongate-rectangular fenestrule.

MATERIAL. Eighty-five specimens of this common, though variable form were examined. They ranged in size from small, virtually complete zoaria about 10 × 5 mm, to a large fragment from the proximal part of a colony measuring 22 × 20 mm. PD.4717–21, PD.4993, PD.4995–9, PD.5009–24.

Measurements (N = 27):

	A	B	C	D
F.l.	0·90–1·57	1·166	0·134	11·54
F.w.	0·55–0·77	0·641	0·059	9·17
I.ap.s.	0·22–0·31	0·260	0·033	12·88
I.n.s.	0·16–0·40	0·292	0·063	21·62
B.w.	0·25–0·35	0·292	0·031	10·77
Ap.d.	0·10–0·12	0·111	0·011	10·00
Diss.w.	0·12–0·27	0·174	0·035	20·26

Micrometric formula: 13–19/7–10//15–20/12–25.

Apertures per fenestrule.

Range of specimen modes:	3	4	5
Distribution of specimen modes:	10	16	1

DESCRIPTION. The fragmentary specimens indicate that complete zoaria were large, roughly planar, fan-shaped expansions. Several showed parts of basal holdfasts that anchored colonies in position. These vary in size according to that of the colony, larger ones being stout and thickly encrusted with secondary schlerenchyma.

At their lower ends holdfasts may separate into three or four main 'root' processes, with a number of slimmer ancillary ones. The extremities of these expand into thin sheet-like masses that coated objects to which they were attached.

Branches vary in thickness according to age. In the proximal parts of colonies they may be gently sinuous and laterally divergent; medially they tend to be straight and parallel. In most cases branches have a clearly-defined median ridge which, in the proximal region, may be thickly covered with secondary tissue and therefore prominent. The branch surface slopes steeply away on each side of the ridge and, as the under side is shallowly rounded, the cross-section is roughly triangular. Well-developed longitudinal striae are commonly present on the reverse, and ridges between these bear numerous tiny punctae or papillae 0·01–0·03 mm in diameter. These are aligned in poorly defined rows and commonly about 0·06–0·11 mm apart. The reverse may be thickly coated with secondary material and as this increased in thickness it appears to have spread up the flanks of branches from below. At a certain stage zooecial apertures, situated between this advancing front and that which enlarged the keel, came to lie in a groove below and parallel with the latter. Some specimens show that the space between apertures later became thickened also, and in such cases the transverse section of a branch is oval.

Dissepiments are characteristically short, and thinner than branches (commonly a half to two-thirds of the branch width). They are roughly circular in section and striated lengthways. The dissepiments are distinctly depressed below branch level on the obverse, but almost flush with it on the under side.

Except in the proximal region and at bifurcations the fenestrule shape is rectangular. Fenestrules are commonly 2 or 3 times as long as they are wide, the greatest relative lengths being found in the proximal region. Distally, branches spread out and the width tends to increase slightly. Fenestrule margins are mostly straight, but may have a sinuous outline where peristomes are strongly developed and project from a branch.

Zooecial apertures are circular and, when well preserved, bear plain, low peristomes. On parts of some specimens the outer sides of peristomes are strongly developed and the flank of a branch below each is slightly inflated. Owing to this condition the branch margin is beaded and not straight. Some branches show a tendency for a regular arrangement of zooecial apertures, with one opposite the end of each dissepiment and 2 to 4 others bordering the intervening fenestrule. This is by no means general, however. Zooecial chambers are mostly triangular in plan, though in some cases the presence of short lateral walls give a shape that is just hemi-hexagonal, and in others the apex of the triangle is truncated so that the shape is best described as trapezoid.

Spacing of carinal nodes on the median keel shows considerable variation from one specimen to another, counts of from 12 to 25 per 5 mm being recorded. Node bases, marking the former position of carinal nodes, are circular or oval (with length parallel to the branch axis) and commonly 0·07–0·1 mm across. Nodes, where present, are not much higher than wide, though some attain a height of 0·15 mm. In the proximal parts of colonies node bases may appear as a row of dark perforations along the crest of a much-thickened median keel. On the reverse a few specimens showed a number of low, rounded swellings or nodes. Though not regularly distributed, there is a tendency for these to be situated opposite branch-dissepiment junctions.

Stout spines diverge from the meshwork on both obverse and under sides of several specimens. Their occurrence seems to have been confined to the proximal parts of colonies. Although all such spines have been truncated by breakage, those on the obverse are longer and stouter than the others. On the obverse, spines are up to 6 mm long, with a basal diameter of 0·45 mm, while on the reverse the greatest length is 3 mm, with a diameter of 0·35 mm.

The presence of thick secondary encrustations, particularly in the proximal region, is characteristic of this form and contributes to the unusual degree of dimensional variation shown by specimens. Such encrustation is not confined to the older parts of colonies, however. In two specimens sections of branches were thickly encased in secondary tissue so that the exterior was quite smooth, and numbers of zooecial apertures were completely sealed. On the proximal side of such sections branches were of normal size and apertures unaffected. Another specimen showed a heavily 'calcified' region close to the distal margin of the colony, as indicated by the presence of unbroken branch tips. The reason for such excessive localized secretion of secondary skeletal material is unknown.

DISCUSSION. These specimens agree in all essentials with Miller's (1961 : 225–228) revised description of *Fenestella plebeia* M'Coy, for which he gave the formula 15–20/8–10//17–20/10–20. It will be noted that the specimens measured by Miller (4 homeotypes) also showed considerable variation in node count. One of them (NMD. XXVIII, II) was collected at Black Lion, about 10 miles from Carrick Lough, and from roughly the same horizon ('Upper Limestone') as the specimens discussed here. Miller stated (p. 226) that the shape of the zooecial chamber base is hemihexagonal, but his illustration (pl. 24, fig. 1) clearly shows shapes that are here called triangular. Some of the Carrick Lough specimens have larger fenestrules than those measured on the type material by Miller, and call to mind Nikiforova's (1927 : 251) *F. plebeia* var. *longifenestrata* from the Lower Carboniferous of the Donetz Basin. However, her illustration (pl. XIII, fig. 2) shows chamber base shapes that approach rectangular and differ greatly from those of the present specimens.

Although Ulrich (1890 : 537) commented on similarities between *F. rudis* and *F. plebeia*, and Miller (1961 : 228) thought that the two might be conspecific, the writer sees closer resemblances between M'Coy's species and *F. compressa* Ulrich. The latter approaches more closely to *F. plebeia* in having rather more carinal nodes and fewer zooecial apertures per unit distance than *F. rudis*, also in having more apertures per fenestrule (3 to 4, as against 2), longer and narrower fenestrules, and branches that are slimmer in relation to fenestrule width. Laterally compressed branches with outward-facing apertures, and the presence of a clear median keel in *F. compressa* also invite close comparison with *F. plebeia*, whereas corresponding features in *F. rudis* have a distinctive appearance. *F. demaneti* Kaisin also shows close resemblances to *F. plebeia*. Kaisin did not identify the latter species from the Tournaisean of Belgium, though it could reasonably have been expected in those strata, but Kaisin (1942 : 105) did list *F.* aff. *compressa.* He differentiated *F. demaneti* from this form only on the basis of its more closely spaced branches (16–17 as against 14–15). Division of the two might have been rendered more convincing if some indication had been given of the number of specimens measured. In any case, as the range of branches per 5 mm in *F. plebeia* is 15–20 it seems possible that Kaisin's material really belonged to that species. The micrometric formulae of the forms discussed are as follows:

	Br/10	*F*/10	*Ap*/5	*N*/5
F. plebeia. (Type specimens)	15–20	8–10	17–20	10–20
F. plebeia. (Carrick Lough)	13–19	7–10	15–20	12–25
F. rudis, Ulrich 1890	16–18	10	20–21	14–16
F. compressa, Ulrich 1890	14–15	8½	16–18	about 16
F. aff. *compressa.* (In Kaisin 1942)	14–15	8–10	18	16–18
F. demaneti, Kaisin 1942	16–17	7–9	18	17

Fenestella cf. ***arthritica*** Phillips

(Pl. 7, figs 8–9; Pl. 8, figs 1–4)

Material. More than 50 zoarial fragments of this moderately common form were examined, the largest measuring 30 × 15 mm. Proximal, medial and distal parts of colonies were all represented. PD.4722–28, PD.5025–37.

Measurements (N = 20):

	A	B	C	D
F.l.	1·20–1·50	1·410	0·087	5·46
F.w.	0·80–0·11	0·935	0·077	8·23
I.ap.s.	0·31–0·35	0·324	0·013	4·17
I.n.s.	0·45–0·67	0·531	0·045	8·47
B.w.	0·35–0·45	0·414	0·025	6·16
Ap.d.	0·10–0·15	0·120	0·115	9·58
Diss.w.	0·17–0·30	0·211	0·031	14·67

Micrometric formula: 10–13/7–9//14–17/8–11.

Apertures per fenestrule.

Range of specimen modes:	3	4
Distribution of specimen modes:	5	15

Description. The fragments showed a strong, compact meshwork of medium texture. Their shapes suggested that complete zoaria were more or less planar, fan-shaped expansions of intermediate size (say, 3 to 6 cm across).

Branches are straight or gently curving, with relatively few bifurcations. They are broad for the meshwork texture and flattened on the obverse, though with a strong median ridge or keel. Proximally, branches may be encased in secondary schlerenchyma which in some cases obscures the median ridge and results in a stoutly rounded cross-section. Such branches may have widths up to 0·57 mm.

The reverse is in most cases broadly rounded and may have a fibrous appearance, though longitudinal striae of the orthodox kind were not seen. A few specimens showed rows of minute papillae parallel with the branch axis.

Dissepiments vary considerably in length and width, but are commonly short and about half as wide as branches. The width may, however, be much increased by secondary encrustation and in the proximal part of a colony may attain 0·45 mm. Dissepiments widen notably towards the junction with a branch. They are slightly depressed below branch level on both surfaces and broken ends commonly show an oval cross-section. Because dissepiments increase in width towards the union with a branch, fenestrules are mostly elongate-oval or rectangular with rounded extremities. Their long sides are in most cases straight, but may be slightly indented by protruding peristomes.

Zooecial apertures are circular, relatively small, and directed upwards and away from the branch. Some specimens show apertures with plain, circular, collar-like peristomes, particularly in the encrusted proximal part of colonies. Where peristomes are well developed they may protrude slightly into fenestrules. The zooecial chamber plan varies from hemi-hexagonal to near rectangular, and a prominent hemiseptum is developed. Average dimensions of eight hemi-hexagonal chambers were: length, 0·35 mm; width, 0·18 mm. Corresponding dimensions of four rectangular chambers were: 0·32 mm and 0·16 mm respectively.

Carinal nodes, when well preserved, are tall and spaced fairly regularly along the median keel. In profile they resemble the teeth of a saw, and may attain a height of 0·37 mm (about the same as that of a branch). These nodes or spines are cylindrical in the upper part, with a diameter of about 0·12 mm, but laterally compressed below. The spine-base is oval with the long axis (about 0·17 mm) parallel to the branch. The distal ends of spines, which are always broken, may show a hollow axial cavity about 0·05 mm across.

A few specimens had nodular swellings on the reverse of branches. These were commonly about 0·02 mm in diameter and formed a somewhat irregular row along the mid-line, approximately 0·2 mm apart. In some cases distribution appeared to be random. The stumps of stout spinose processes are present on the obverse and reverse of some fragments, particularly in the proximal region, and one or two specimens showed strong lateral spines developed as continuations of ordinary branches.

Discussion. This form bears strong resemblances to *Fenestella arthritica* Phillips 1841, originally recorded from the Middle Devonian. The types of this species have been lost for many years and the author's description and illustrations are inadequate by modern standards. Nevertheless, the present specimens correspond with them as far as they go. For example, Phillips mentioned the presence of thick branches and dissepiments with oval fenestrules, and his illustration clearly shows the hemi-hexagonal zooecial chambers. Whidborne (1895 : 170–172) subsequently identified the species from the Middle Devonian of north Devon and his account is valuable, as he was familiar with the type material. Whidborne's description is more comprehensive than that of Phillips and includes some measurements (about 8 fenestrules and 13–15 branches in 10 mm) with which the Carrick specimens are in reasonable agreement. He noted that branches are commonly rather narrower than fenestrules, and that they divide only at distant intervals. He also observed the tall carinal spines, though he only saw these in thin section and consequently mistook them for a high, thin keel running the length of the branch. He commented on the presence of nodes on the reverse (pl. XIX, fig. 6) and of 3 to 5 zooecial apertures along each fenestrule margin. Elias (MS. 1950 : 1) identified *F. arthritica* from the Lower Limestone Group of Scotland and noted the 'pentagonal' chamber base shape and presence of 4–5 zooecia per fenestrule. He gave the following formula for specimens in the Hunterian Museum collections, Glasgow University: 13/7–8//16–17/8–10. The formula for the material from Carrick Lough is close to this and, in view of the similarities noted above, it seems probable that those specimens are related to *Fenestella arthritica*, if not identical with it. However, because of the absence of type specimens, the imperfections of earlier descriptions and the fact that the original form was Devonian, it seems advisable to leave the identification as a provisional one.

Another species that is morphologically close to the specimens discussed here is *F. nododorsalis* Ulrich, for which Nekhoroshev (1956 : 152) gave the formula: 14/6½–8//15–16/? On the basis of Russian specimens he stated the internodal distance to be 0·35 mm (Table 4, pp. 138–139), suggesting about 14 nodes in 5 mm, a number considerably in excess of that seen on the Carrick Lough material. Ulrich's original specimen, *F. compressa* var. *nododorsalis* (1890 : 540) showed only the reverse surface with 12–13 branches and 7½–8 fenestrules in 10 mm. The parent species *F. compressa* Ulrich, has the formula: 14–15/8½//16–18/ about 16, and is similar in several respects to the Irish colonies though with more carinal nodes per unit distance, and thinner and more closely spaced branches. Kaisin (1942 : 105) assigned to *F.* aff. *compressa nododorsalis* specimens with the formula: 14–16/6–8// 17–18/8–10 and with thicker branches (0·4–0·5 mm) than those described by Ulrich. This form was not illustrated but, judging from the description, it may be very close to that considered here.

Fenestella praemagna Shulga-Nesterenko

(Pl. 8, figs 5–11)

1951 *Fenestella praemagna* Shulga-Nesterenko: 104.

DIAGNOSIS. Small, fan-shaped colonies with open meshwork and lax growth habit. Apertures well separated, usually four per fenestrule. Tall carinal spines branch at their distal ends.

MATERIAL. Twenty-six specimens of this form were examined. Almost all were fragments from the proximal parts of colonies. The largest was 8 × 10 mm. PD.4729–35, PD.5038–46.

Measurements (N = 16):

	A	B	C	D
F.l.	1·05–1·57	1·384	0·131	9·46
F.w.	0·62–0·85	0·730	0·072	9·87
I.ap.s.	0·27–0·35	0·301	0·019	6·48
I.n.s.	0·50–0·75	0·665	0·070	10·56
B.w.	0·25–0·35	0·310	0·030	9·83
Ap.d.	0·07–0·11	0·095	0·016	16·27
Diss.w.	0·15–0·20	0·172	0·016	9·46

Micrometric formula: 12–15/6–9//14–18/6–10.

Apertures per fenestrule.

Range of specimen modes:	3	4	5	6
Distribution of specimen modes:	2	6	7	1

Description. The specimens indicate that complete zoaria were small, compact, fan-shaped structures probably not more than 2 or 3 cm across. The proximal parts of three colonies, complete with basal holdfasts and supporting processes, show that the growth posture was erect or partly erect, and not recumbent. In one case the holdfast is attached to the obverse side of another fenestrate fragment. The meshwork, composed of stout branches and relatively thin dissepiments, has a rather fine texture and branches commonly show a lax and somewhat irregular growth habit. This may partly be explained by the fact that most of the specimens are from the proximal parts of colonies.

The obverse of each branch bears a fairly well-developed median ridge or keel, from which the surface slopes steeply towards the branch margin. The reverse is rounded and commonly shows a number of fine, closely-spaced, longitudinal striae. In some cases these are also seen on the flanks and upper surface of a branch between zooecial apertures and carinal nodes. Striae in the latter situation are gently sinuous and not strictly parallel with the axis of growth. The broken ends of branches show a transverse section that varies from near-triangular to near-circular.

Dissepiments are relatively slender and bar-like. They do not increase much in width at either end. The cross-section (as seen in broken ends) may be roughly circular or oval, with the long axis either horizontal or vertical, depending on whether the width or height is greater. Dissepiments are slightly depressed below branch level on both sides and may be rather irregularly spaced, as is usual in the proximal parts of zoaria.

Fenestrules are commonly one-and-a-half times to twice the width of branches and their shape is basically elongate-rectangular with rounded extremities. However, due to the lax growth habit of branches and their recurrent division (associated with the proximal location of most of the fragments), and also to the somewhat irregular placing of dissepiments, fenestrule shapes vary considerably and may be rectangular, quadrate or even elliptical.

Zooecial apertures are situated in two rows placed well out towards branch margin and away from the median ridge. Apertures are relatively small, circular and well-separated (between 1½ and 2½ diameters apart). Peristomes may be present as plain, circular, collar-like rims. These may project slightly from the branch margin, giving the latter a sinuous or scalloped aspect. Slight localized inflations along the flank of a branch immediately beneath each zooecial aperture may emphasize this appearance, particularly on the reverse.

The internal structure is poorly preserved and only seven zooecial chambers were measured. Of these, five had a triangular plan (maximum length: 0·3 mm; width: 0·17 mm) and the others were trapezoid, with the longest side 0·27 mm, shortest side 0·1 mm, and the perpendicular distance between them 0·17 mm.

Carinal nodes are unusually well-developed, and placed at fairly regular intervals along the keel. They are tall, slender, and at their distal ends divide into a number (commonly four) of separate processes, or tines. Although the broken stumps of nodes show the usual axial hollow, the distal ends of unbroken tines are sealed, with no sign of perforation. Complete nodes are taller than the branch bearing them (up to 1·37 mm against 0·32 mm) and commonly have a basal diameter of about 0·16 mm.

Three specimens with the basal holdfast preserved also show subsidiary supporting processes. These are slender columns up to 4 mm long dividing at their ends into short digitate processes which are attached to the substratum. Such processes and their 'arms' would, if found separately, show a close resemblance to the form genus *Palaeocoryne*.

In a few specimens small nodes are arranged uniserially along the mid-line of parts of the reverse surface. These pimple-like swellings have a diameter of about 0·05 mm and are spaced about 0·12–0·17 mm apart. Larger nodes occur at random on the under side of branches, being most commonly situated in the angle at branch divisions and at branch-dissepiment junctions. They are 0·12–0·17 mm in diameter and have the shape of cones up to 0·17 mm high.

DISCUSSION. The well-developed carinal nodes in this form, with their relatively regular spacing and branching ends, suggest an intermediate stage between the simple, pillar-like nodes of most *Fenestella* and the symmetrical superstructure of *Hemitrypa*. The coefficient of variation for internodal distance is here 10·56; that of specimens of *Hemitrypa hibernica* was 6·71, while the figure for species of *Fenestella* is mostly between 13 and 23. Increased regularization in the spacing of carinal nodes and union of branching distal extremities may well have led to the formation of geometrically ordered superstructures, such as that of *Hemitrypa*. Chronic (1949 : 117) described branching carinal nodes in the fenestrate form *Cervella cervoidea* from the Lower Permian of Peru, and Elias & Condra (1957 : 109) found the same feature in *Fenestella cornuta* from the Wolfcamp (early Permian) of the Glass Mountains, Texas. In these cases also, authors noted the rounded and imperforate ends of the branching tines, making it appear certain that they did not house acanthopores, as has sometimes been supposed (e.g. Ross 1961: 68).

In appearance and dimensions the present specimens correspond closely with Shulga-Nesterenko's (1951 : 104) *Fenestella preamagna* from the Upper Carboniferous (Gzhelian) of Russia, and are assigned to that species. The formula given by that author is: 13–14/6–7//15–16/7½–10, and the number of zooecial apertures per fenestrule 4 or 5. It is stated that *F. preamagna* has oval apertures, but this is not commonly the case with the Irish specimens, though in one or two fragments apertures were slightly elongated transversely. Shulga-Nesterenko noted the presence of large carinal nodes, but did not mention any peculiarity in their shape. This is not surprising, as her material was not silicified and the spines were probably broken off near branch level.

There is also some similarity between the Fermanagh specimens and *Fenestella varifenestrata* Elias & Condra 1957, from the Lower Permian (Upper Leonard) of Texas. However, that species was founded on a single small, poorly-preserved specimen and it is not possible to make a worthwhile comparison. The authors gave the formula: 12/10//16/7–8, with 2 to 5 apertures per fenestrule. The presence of tall, stout nodes on a weak keel, and small, rather widely spaced apertures are features in agreement with the Fermanagh specimens, but no information was given regarding branch width, zooecial chamber shape or other characteristics, and the illustrations are uninformative (pl. 10, figs 1–4). It is possible, however, that Elias and Condra's specimen is itself referable to *F. preamagna*.

It would appear that the Fermanagh specimens are most closely comparable with Upper Carboniferous and Lower Permian species. This may, therefore, be a case in which the Carrick residues contain early members of stocks that later became widely dispersed.

Fenestella fanata Whidborne ***carrickensis*** subsp. nov.

(Pl. 9, figs 1–9)

Material. This is a moderately common form and more than 100 fragmentary specimens were examined. The largest measured 22 × 24 mm. The form is particularly interesting because of the presence of large numbers of inflated ovicells. These have been described elsewhere (Tavener-Smith 1966a). PD.4736–42, PD.5047–67.

Measurements (N = 28):

	A	B	C	D
F.l.	1·07–1·62	1·329	0·119	8·95
F.w.	0·70–1·02	0·848	0·757	8·93
I.ap.s.	0·35–0·45	0·383	0·023	6·07
I.n.s.	0·42–0·75	0·555	0·084	15·13
B.w.	0·33–0·47	0·400	0·035	8·80
Ap.d.	0·12–0·19	0·151	0·016	10·74
Diss.w.	0·17–0·37	0·233	0·040	17·38

Micrometric formula: 10–13/6–9//10–14/6–11.

Apertures per fenestrule.

Range of specimen modes:	3	4
Distribution of specimen modes:	26	2

Diagnosis. Zoarium a flabellate expansion of rigid branches with a distinctive bifurcation pattern and roughly circular cross-section. Keel obsolescent, carinal nodes small and distantly placed. Apertures in two alternating rows placed close to the median line. Zooecial base shape hemi-hexagonal. This form is distinguished from *F. fanata* s.s. by its distinctly narrower branches (about 0·3 compared with 0·4 mm), reduced inter-apertural distance (about 0·3 as against 0·383 mm) and shorter, more compact zooecia.

Type specimens. Holotype: PD.4736. Paratypes: Other zoarial fragments numbered PD.4737 to PD.4742.

Description. The sample includes fragments from all parts of colonies except the proximal extremity. They suggest that entire zoaria were roughly planar or somewhat foliaceous, flabelliform expansions, such as that illustrated by Whidborne (1895: pl. XVIII, fig. 6).

The meshwork consists of stout, straight branches and thin dissepiments bounding rectangular or oval fenestrules. A distinctive feature is the presence on branches of globose ovicellular inflations commonly incorporating more than one zooecial aperture. These may be situated at branch-dissepiment junctions, in which case the dissepiment is also variably inflated. Ovicells may be associated in groups on adjacent branches, and pairs are commonly in juxta-position, being partially fused, or conjoined.

Branches are approximately circular in cross-section with no noticeable keel and the reverse may bear faint longitudinal striations. The bifurcation pattern shown by branches and zooecial apertures is distinctive. For two or three fenestrules prior to division branch widths may increase to a maximum of about 0·9 mm. Immediately thereafter the width of each new branch is reduced to about 0·35 mm. The abnormally wide section on the proximal side of the fork is flattened dorsi-ventrally and bears an extra row of apertures. This 'third row' may be up to 4 or 5 apertures long, and the appearance in this part of a branch may be similar to that of *Polypora*. The arrangement of apertures may be quite regular, with two adjacent rows alternating in the usual manner and an apparently unrelated third row on one side of them, or it may be somewhat irregular. In a few fragments the third row is represented by only a single extra aperture in the angle of bifurcation. In such cases the preliminary expansion of the branch is also much reduced and the pattern resulting from division is more like a wish-bone than a steep-sided V.

Dissepiments are straight and bar-like in the distal parts of zoaria; only slightly expanded at their extremities and moderately depressed below branch level on each side. In the proximal region they are relatively shorter and stouter, with considerably expanded ends and only slightly depressed on the obverse, though more so on the under surface. The transverse section of young dissepiments is roughly circular, though it is commonly oval in older ones. Where an ovicell is situated at or near a branch-dissepiment junction the dissepiment tends to be greatly enlarged over much or all of its length.

Fenestrule shape and size in this form are greatly influenced by age. In the younger parts of colonies relatively large rectangular fenestrules with rounded extremities are bounded by branches and dissepiments of moderate dimensions. In the older parts, the strong, close-textured meshwork is composed of notably stouter elements and, because dissepiments flare at their ends, fenestrules are mostly elongate-oval. Zooecial apertures never project beyond branch margins and the long sides of fenestrules are therefore straight.

Apertures are mostly circular, but may be semi-oval or reniform. In the last two cases the major convexity is always distal. Apertures are relatively large and the two alternating rows placed close to the mid-line and away from the branch margin. The inner limits of apertures in opposed rows reach the mid-line in most specimens. There is, therefore, no room for a longitudinal median ridge of the orthodox kind, and the crestal part of a branch assumes a zig-zag pattern between the apertures of opposite rows.

The zooecial base-plan is hemi-hexagonal, but at higher levels longitudinal sections show an almost rectangular shape. This is because the base-plan relates only to a proximal chamber about 0·3 × 0·2 mm which forms the lower part of a zooecium (Tavener-Smith 1966a : 192, text-fig. 1A). Above it the latter is continued as an elongate tube obliquely inclined (at about 25°) for most of its length but curving sharply towards the branch surface distally to form the vestibule. The mean length of 20 measured zooecial tubes was 0·85 mm, and the width 0·16 mm. A shelf-like hemiseptum is present at the base of the vestibule.

Carinal nodes are small, distantly placed and difficult to identify. They are low in comparison with branch height (0·1 mm compared with about 0·4 mm). The nodes are uniserial, each being situated on a low oblique ridge separating two apertures in opposite rows. Nodes of unusually large size commonly surmount ovicellular inflations. There may be a single one, centrally placed, or a pair, with one at each end of the swelling.

Discussion. The specimens described are morphologically close to Whidborne's (1895 : 165–168) *Fenestella fanata* from the Middle Devonian of north Devon. The formula of that species, derived from Whidborne's description, is: 10–15/6–9// about 17/?, and the number of apertures per fenestrule 3 or 4, mostly 4. The zoarial shape, spacing of branches and fenestrules, and the peculiar bifurcation pattern described by that author are identical to those of the Fermanagh specimens. Whidborne particularly commented on the last feature (p. 166) and mentioned a remark by Gregory about the similarity to *Polypora* at branch divisions. The rounded cross-section of branches, fenestrule shape and virtual absence of median keel and carinal nodes are other important features common to both forms. The hemi-hexagonal zooecial base-shape is another point in common, though comparison with the types (kindly loaned by the Curator of the Sedgwick Museum) shows that the zooecial chambers differ. In the Devonian specimens branches are thinner (average of 24 measured: 0·3 mm) and the inter-apertural distance less (average of 12 measurements: 0·3 mm). Zooecia are, therefore, shorter and more compact than in the Fermanagh material, and the hemi-hexagonal shape of the chamber base is continued above, though there is a tendency towards a rectangular shape at the upper levels.

The morphological resemblances noted are, in the writer's opinion, strong enough to justify placing the present specimens in *Fenestella fanata*, but recognition must be given to the important differences in zooecial size and shape. Hence, it is proposed to introduce a new subspecific name, *carrickensis*, for the Fermanagh form.

***Fenestella* cf. *spinacristata* Moore**

(Pl. 10, figs 1–6)

MATERIAL. Fifty-four fragments were examined, mostly from the proximal and medial parts of colonies. The largest was 20 × 15 mm. PD.4743–50, PD.5068–84.

Measurements (N = 25):

	A	B	C	D
F.l.	1·15–1·62	1·353	0·125	9·27
F.w.	0·65–0·90	0·745	0·064	8·59
I.ap.s.	0·26–0·32	0·293	0·023	8·02
I.n.s.	0·35–0·60	0·429	0·058	13·53
B.w.	0·22–0·30	0·250	0·021	7·20
Ap.d.	0·10–0·12	0·110	0·008	7·27
Diss.w.	0·12–0·22	0·160	0·023	14·69

Micrometric formula: 11–14/6–7//13–17/6–15.

Apertures per fenestrule.

Range of specimen modes:	3	4
Distribution of specimen modes:	12	13

DESCRIPTION. Fragmentary specimens examined indicate that complete colonies were fan-shaped expansions of medium size with an erect or party erect posture. A basal holdfast, of which vestiges are preserved in some specimens, secured each colony in position.

Branches are slender and relatively widely spaced, so that the meshwork has an open texture. They may be gently sinuous, giving a rather lax appearance, but are commonly straight and rigid-looking. Branches are narrow in relation to their height (mean width: 0·25 mm, mean height: 0·3 mm, both of 25 specimens) and on the obverse the surface slopes steeply away from a clearly defined median keel. The under side is rounded, so that in transverse section the shape is that of a high triangle with a rounded base. The pattern formed at branch divisions is distinctive: at first the new branches diverge sharply, but after a short distance they curve into parallelism once more, so that a wish-bone shape is formed. In the proximal region, and whenever a thick coating of secondary schlerenchyma is present, the keel may become greatly thickened and present a prominent, cord-like appearance.

Dissepiments are thin, straight and bar-like. They are commonly little more than half the branch width, show a circular cross-section and do not widen much at either end. Dissepiments are strongly depressed below branch level on the obverse, but flush with it or only slightly depressed on the reverse side. The relatively distant spacing of dissepiments contributes to the open-textured meshwork of this form.

The shape of fenestrules (away from branch bifurcations) is rectangular, though the proportion of width to length varies. In the proximal region, where branches are most closely spaced, it may be as great as 1 : 4, while in distal parts of the mesh it may be only 1 : 1½. Proportions of 1 : 2 or 1 : 2½ are commonest.

Zooecial apertures are circular, or rarely reniform in older parts of colonies, and may show low, rim-like peristomes projecting slightly into the fenestrule. Apertures are 1½–2 diameters apart and directed laterally into the fenestrule from the steeply sloping flank of a branch. Viewed microscopically the regular spacing and lateral aspect are reminiscent of port-holes in the side of a ship. Apertures are not stabilized with respect to dissepiments, and from 3 to 6 may occur in the length of a fenestrule. Zooecial chamber bases are trapezoid, the average dimensions of 17 being: long side, 0·17 mm; short side, 0·1 mm (both measured parallel with the branch); width, 0·15 mm.

A single row of peculiarly-shaped carinal nodes is situated along the median keel. They are relatively small, widely spaced and commonly inclined towards the growth origin. Nodes are about 0·12 mm in diameter at the base and taper upward to about the same height. On the reverse a few specimens show sporadically-developed nodes of small size, 0·15–0·25 mm apart along the mid-line. These are about 0·04 mm in diameter and of about the same height. They are not present on dissepiments.

Discussion. A strong indication of the growth habit of colonies of this kind is provided by a specimen attached to a *Penniretepora* stipe. The fenestrate colony originates in a mass of 'calcareous' material that embraces the *Penniretepora* and acts as a holdfast. Branches radiate from this, and those along one margin of the newly-developing colony curve back towards the *Penniretepora* and re-unite with it for support. It is reasonable to suppose that the stick bryozoan either lay on the sea bed or grew in an upright position. In neither case could the attached *Fenestella* have been recumbent, and it appears to have had an erect or near-erect posture.

An example of the protective function of the keel and carinal nodes is given by a specimen bearing a small, button-like colony of *Fistulipora* on the obverse. The under side of the latter is not everywhere welded onto the fenestrate branches, but is only attached at a few points. Elsewhere, there is a clear space between the two and, as the apertures of the *Fenestella* are unsealed, it is likely that they continued to function in spite of the overlying *Fistulipora*. Immediately above the keel and nodes on the fenestrate branches there are corresponding depressions in the basal lamina of the *Fistulipora*, and it seems probable that those features caused the latter to 'keep its distance', thus allowing enough space for the polypides to be extruded. It is easy to see that a uniformly developed superstructure, such as that of *Hemitrypa*, would perform the same service much more effectively.

Features that distinguish fragments of this kind from other fenestrate species in the residues are (in addition to the meshwork dimensions) the slim branches with steep-sided triangular cross-section, forming an open-textured mesh, the zooecial apertures, suggesting in their close and regular arrangement a line of port holes, and the small, inclined and widely spaced carinal nodes. Among described species the form is closest to *Fenestella spinacristata* Moore 1929, from the Pennsylvanian of Kansas. The micrometric formulae are essentially comparable (that based on Moore's description being: 13–14/7–9//14–16/12–14), though the fenestrules in *F. spinacristata* are slightly narrower and the carinal nodes more distantly placed. In both the nodes are laterally flattened and inclined proximally. Moore's specimens had a branch width of 0·45–0·55 mm, however, much in excess of that of the Fermanagh material, though it is possible that his fragments were old and heavily encrusted. It is felt that although the resemblance to *F. spinacristata* is in some respects marked, discrepancies of branch width and fenestrule size prevent the firm assignment of the Fermanagh specimens to that form.

Another possibility, though remote, is that this form is a variant of *F. plebeia* M'Coy, to which there are certain qualitative resemblances. There is only slight overlap between the formulae, however, due to the more open texture of the present specimens. The existence of significant ($P < 0{\cdot}05$) statistical differences between the two samples in matters of fenestrule length and width, branch width and interapertural space also make it impossible to equate them.

***Fenestella* cf. *funicula* Ulrich**

(Pl. 10, figs 7–10; Pl. 11, figs 1–4)

Material. This is a common form, and more than 120 zoarial fragments were examined. A sample of 25 of the best preserved was selected for measurement. The largest specimen had a size of 26 × 16 mm. PD.4751–59, PD.5085–5100.

Measurements (N = 25):

	A	B	C	D
F.l.	1·07–1·70	1·421	0·126	8·85
F.w.	0·67–0·92	0·776	0·066	8·50
I.ap.s.	0·29–0·34	0·312	0·011	3·48
I.n.s.	0·47–1·00	0·704	0·124	17·69
B.w.	0·30–0·40	0·342	0·025	7·39
Ap.d.	0·09–0·12	0·103	0·011	10·58
Diss.w.	0·16–0·25	0·197	0·021	10·89

Micrometric formula: 10–14/5–9//13–17/4–9.

Apertures per fenestrule.

Range of specimen modes:	3	4	5
Distribution of specimen modes:	8	16	1

Description. The complete zoarium appears to have been an approximately planar, fan-shaped expansion. Branches are straight or slightly sinuous, with a median keel that may be prominent and rib-like in the older parts of colonies, due to selective deposition of secondary schlerenchyma. Branch sides slope steeply away from the keel and the under side is broadly rounded. The latter commonly shows fine, closely-spaced longitudinal grooves and ridges, with a row of minute papillae (the 'capillaries' or 'granulations' of Russian authors) at intervals of about 0·04 mm along the crest of each ridge. Clearly defined striations are not seen on the obverse, but this side (particularly the keel) may show numbers of short, sinuous ridges, each bearing a row of papillae corresponding in appearance with those on the under side. In the older parts of zoaria branches may be thickly coated with secondary material showing parallel ridges, each bearing a row of papillae. This external cover may seal up zooecial apertures and give branches a roughly circular cross-section instead of the commoner triangular one. On the reverse of branches there may be a variable number of low nodes or short, pointed spines. These are situated along the mid-line, particularly opposite branch-dissepiment junctions, or in the angle where branches divide. They are of irregular distribution, and present on only a few specimens.

Dissepiments are from half to two-thirds the width of branches. They have a circular cross-section and widen considerably at their ends. Most dissepiments are clearly depressed below branch level on the obverse, but flush with it, or only slightly depressed, on the under side. There may be a series of closely spaced ridges and grooves along the length of a dissepiment, and these merge at either end with those on branches. The ridges may each bear a crestal row of minute papillae.

Fenestrules vary considerably in shape and size, particularly in the proximal region. They are commonly rectangular or elongate-oval, and about 2 or 3 times as long as wide.

Zooecial apertures are mostly circular but may be reniform in the older parts of colonies. They are small and relatively widely spaced (2 or 3 diameters apart). Low, collar-like peristomes surround apertures in some specimens and may project slightly into fenestrules, giving the long sides of the latter a beaded appearance. The zooecial chamber is a box-like structure with hemi-hexagonal plan and walls which (except the outer one) are inclined distally. It is as if the box had received a blow from one side. Average dimensions of 20 chamber bases were: maximum length, 0·32 mm; maximum width, 0·16 mm.

Tall, stout carinal nodes or spines rise from the median keel and, even when not seen, their former presence may be inferred from elliptical spine-bases. The major axes of these are parallel with that of the branch and 0·12–0·2 mm long. Spines are circular in cross-section and up to 0·82 mm high, though invariably broken at the distal end. Many are seen to be hollow, with an axial cavity about 0·07 mm in diameter extending down into the branch. Spines that are longer and stouter than carinal nodes are present on some fragments. They rise from the median keel and, though broken distally, may attain a length of 6 mm. They have a circular transverse section and on the exterior show a fine ribbing parallel with their length. The ribs, or striae, merge with those of the keel and along their length carry minute, closely spaced papillae identical to those on branches and dissepiments.

One specimen showed an aberrant branch which, possibly because of injury, grew upward from a branch division at right angles to the zoarial plane. After 1·5 mm in this direction the branch gave rise, on its dorsal side, to a stout spine of the kind described above. This grew back towards the zoarial mesh at about 45° and, by uniting with the latter, afforded support to the aberrant branch. Where the supporting process met one of the branches of the meshwork its substance grew over the latter but did not merge with it. This is clearly shown by the ridges and grooves on the spine end: they do not fuse with corresponding features on the branch, but form a number of discrete dactylose processes that clasp the branch and firmly secure the spine to it.

On some fragments spinose processes arise laterally as branch continuations at the zoarial margin. Where a change of this kind takes place zooecial apertures cease, the branch shows a slight decrease in diameter, and the exterior assumes a uniformly striated appearance.

Discussion. The presence of strong carinal nodes with hollow axial tubes recalls the suggestion of some authors (e.g. Condra & Elias 1944 : 26; Ross 1961 : 68; Miller 1961 : 223) that such nodes housed acanthopores or similar structures. The writer has carefully considered this possibility but concludes that there is no evidence to support the idea. The probability seems to be that the nodes were originally solid (the axial hollow having contained primary skeleton) and their ends imperforate. Being tall and pointed it would appear that their function was to prevent browsing predators from approaching too closely to the extended polypides of the colony.

The presence of nodes on the reverse of some specimens, but not others, strengthens the suggestion that this feature is of no diagnostic importance. Ulrich (1890 : 540) used it to establish the form *F. compressa* var. *nododorsalis* on the basis of a single specimen of which only the reverse could be seen. In the Carrick Lough collection several species included specimens with and without such nodes.

External ribs and grooves ('striations') on many specimens are seen to be continuous between branch and dissepiment, but this is not so in the case described above where a spinose process united with a branch of the same colony. The difference seems likely to be due to physiological controls that operated within the colony. The purpose of dissepiments appears to have been the provision of *internal* support by acting as bracing struts between branches. Therefore, although each dissepiment probably originated as a pair of opposing outgrowths on adjacent branches, these were able to fuse to form the cross-bar, and striae become continuous across them. Spinose processes, on the other hand, are here interpreted as structures intended to afford *external* support for the colony by attachment to convenient neighbouring objects. Such attachment, for obvious reasons, could not have been attained by organic fusion and was effected instead by the prolific secretion of secondary schlerenchyma. This formed an enveloping crust around the foreign body, or a number of dactylose processes which clasped it. Thus, even when a supporting spine encountered another part of its own colony union was effected as if with some external object. Such unions commonly resulted in appearances closely resembling that figured by Vine (1879 : fig. 203) as 'the base of a *Palaeocoryne*-like pillar parasitically attached to *Fenestella* sp.'. It seems likely that *Palaeocoryne* and its allies are to be explained by such relationships.

The specimens show important resemblances to *Fenestella funicula* Ulrich 1890, from the Keokuk Group (probably lower Visean) of Iowa. The formula of this species is: 14–15/about 5//13/about 7, and there are 4 to 6 apertures per fenestrule. *F. funicula* appears to have longer fenestrules and more widely spaced apertures than the Fermanagh material, though these could be peculiarities of the single small specimen illustrated by Ulrich (pl. LI, fig. 6) and upon which his description appears to have been based. He noted that it was a rare form. Ulrich commented on the strong keel carrying widely spaced nodes, but otherwise the description is uninformative and it is impossible to make more than a tentative assignment to the species.

There are also similarities with the Upper Carboniferous (C_3^{gz}) *Fenestella ghzelensis* Shulga-Nesterenko 1951, from Russia. The formula of this species is: 11–13/7–8//

15–16/5–6 and the number of zooecial apertures per fenestrule, 3 to 4. Other common features include a strong keel with prominent nodes, and the presence of longitudinal ridges bearing rows of papillae on the reverse. Branches are wider in the Russian form, however, (0·4–0·5 mm compared with 0·3–0·4 mm) and the chamber shape appears (pl. II, fig. 3 and pl. IV, fig. 2) to be more commonly 4- than 5-sided. Also, the Fermanagh specimens do not show smaller nodes between each pair of large ones on the keel, as described by Shulga-Nesterenko.

Fenestella placida Moore 1929 also has similar meshwork characteristics to the Irish specimens. This species, from the Pennsylvanian of Texas, has 4 apertures per fenestrule and the formula is: 10/6//15–16/3–10. It appears to differ from the Fermanagh material in having larger fenestrules (average: 1·5 × 0·6 mm compared with 1·2 × 0·43 mm), thinner dissepiments (only 0·06–0·1 mm wide) and a more flattened obverse branch surface. Carinal nodes are notably smaller and zooecial apertures directed upward rather than laterally, as in the Carrick Lough specimens.

***Fenestella* cf. *filistriata* Ulrich**

(Pl. 11, figs 5–10; Pl. 12, fig. 1)

MATERIAL. This is a moderately common form with a medium-textured meshwork. More than eighty fragments were examined, of which the largest was 23 × 14 mm. PD.4760–64, PD.5101–5120.

Measurements (N = 25):

	A	B	C	D
F.l.	1·50–2·10	1·776	0·164	9·23
F.w.	0·75–1·00	0·878	0·069	7·86
I.ap.s.	0·26–0·32	0·295	0·011	3·65
I.n.s.	0·45–0·70	0·555	0·092	16·55
B.w.	0·30–0·37	0·340	0·023	6·90
Ap.d.	0·06–0·10	0·078	0·010	12·42
Diss.w.	0·12–0·22	0·186	0·026	14·25

Micrometric formula: 10–14/5–8//16–18/7–10.

Apertures per fenestrule.

Range of specimen modes:	4	5	6
Distribution of specimen modes:	1	19	5

DESCRIPTION. Complete zoaria were probably planar, fan-shaped expansions. There is no certain indication as to whether the growth position was upright or recumbent. In many specimens the meshwork presents a somewhat lax appearance but in others branches and dissepiments are straight and rigid-looking.

Branches are dorsi-ventrally flattened, and the gently curved obverse surface lacks a strong median keel. In its place may be a hair-like ridge bounded by grooves which are in turn flanked by other, fainter ridges and grooves which form a delicate tracery over the obverse of the branch. In some specimens the median ridge is more pronounced and thread-like, and in others it is broader and rounded, forming a low crest from which the branch surface slopes gently to the fenestrule. All gradations between these conditions are to be seen. In the proximal parts of colonies secondary accretions emphasise the median crest, though it remains low and rounded. The reverse of branches is strongly convex and commonly shows about a dozen fine and closely-spaced longitudinal grooves or striae.

Dissepiments are thinner than branches and of variable length and width, being slender rods in one fragment and short, stout bars in another. Many have well developed ridges and striae along their length. Dissepiments are depressed below the branch crest on the obverse, but only slightly, if at all, on the reverse.

Fenestrules are mostly rectangular or elongate-oval, and of considerably greater width than branches. Their long sides may be straight or beaded, the latter appearance resulting from the slight projection of zooecial apertures beyond branch margins.

Two alternating rows of circular apertures are situated close to branch margins and away from the mid-line. They are relatively widely spaced, being two to three diameters apart and, due to the flattened nature of the obverse surface, face almost directly upward. Each aperture has a ring-like peristome which rises slightly above the general surface and, in conjunction with a slight swelling of the side wall, may cause a lateral projection into the fenestrule. At branch divisions a zooecial aperture may be situated symmetrically in the angle of bifurcation. A short extra row of up to three apertures may occur in such positions, but is uncommon.

The zooecial base-shape is irregularly pentagonal, the chamber itself being divided into two parts by a strong, shelf-like hemiseptum. This originates from the dorsal side and is therefore inferior. It has an arcuate plan, and in curving up the outer wall of the chamber provides this with an internal strengthening. Beyond the hemiseptum the wall must be unusually thin, for in the specimens it is commonly breached and the resultant openings give the impression that apertures are twice as numerous as in reality.

Carinal nodes are variably developed and even when present are weak and of obsolete appearance. In a few specimens they are completely lacking but careful examination invariably shows one or two minute oval node-bases, marking their former position. These are most evident where an axial thread forks at a branch division, and in some fragments are not detectable elsewhere. For the most part these nodes are small, low, irregularly situated and difficult to identify. They would readily be removed without trace by weathering.

A few specimens have spinose processes from the obverse or reverse of the meshwork, or as lateral continuations of branches. They are few in number and do not attain large size. Several fragments showed good examples of regeneration following structural damage sustained during the life of the colony. In such cases displaced and twisted sections of meshwork were stabilized by prolific deposits of secondary tissue in the zones of fracture, and broken ends sealed in the same manner.

DISCUSSION. These specimens are close in appearance and dimensions to *Fenestella filistriata* Ulrich 1890, from the Burlington Limestone (probably lower Visean) of Illinois. The absence of a well-defined keel, wide spacing of zooecial apertures and the striated pattern on the obverse surface are points in common with that species. Structural measurements show a good correspondence except that apertures are more closely spaced in the Carrick Lough specimens (15–18 compared with 13–14 in

F. filistriata). In view of this difference the Irish material is not definitely assigned to Ulrich's species. No mention was made of carinal nodes in Ulrich's description of *F. filistriata*, but small obsolete ones of the kind seen in the present specimens may have been completely removed by weathering.

Fenestella subspeciosa Shulga-Nesterenko

(Pl. 12, figs 2–8)

1955 *Fenestella subspeciosa* Shulga-Nesterenko: 121.

Diagnosis. *Fenestella* with open-textured meshwork and rather lax growth form. Rectangular fenestrules have strongly indented margins due to prominence of cowl-like peristomes on apertures. Zooecia mostly trapezoid.

Material. Forty-six zooarial fragments were examined. The largest measured: 17 × 10 mm. PD.4765–9, PD.5121–40.

Measurements (N = 25):

	A	B	C	D
F.l.	1·20–1·60	1·378	0·111	8·02
F.w.	0·60–0·77	0·697	0·049	7·03
I.ap.s.	0·30–0·35	0·321	0·014	4·43
I.n.s.	0·45–0·70	0·589	0·084	14·30
B.w.	0·21–0·30	0·252	0·018	7·24
Ap.d.	0·10–0·14	0·122	0·009	7·55
Diss.w.	0·12–0·22	0·168	0·023	13·64

Micrometric formula: 12–15/5–7//13–16/6–10.

Apertures per fenestrule.

Range of specimen modes:	3	4
Distribution of specimen modes:	10	15

Description. The specimens appear to have formed parts of small, roughly planar, fan-shaped zoaria between 2 and 4 cm across. The meshwork consists of comparatively slender branches with rather widely spaced dissepiments, and has an open texture. Branches show a slightly irregular or sinuous mode of growth which, combined with the large fenestrules, gives the meshwork a characteristically lax appearance.

The obverse branch surface slopes quite sharply away from a low but clearly defined median keel which may have a thread-like aspect. The reverse is broadly rounded and commonly shows fine longitudinal striae. Transverse sections of branches are mostly oval (long axis corresponding with height of branch), but may be almost circular in older parts which are thickly coated with secondary schlerenchyma.

Dissepiments are from half to two-thirds of the branch width and expand (though not sharply) towards the union with a branch. They are circular in cross-section and depressed below the branch crest on the obverse, though not on the reverse. Many dissepiments show longitudinal ridges and grooves parallel to their length. They are not much affected by secondary thickening and commonly present a marked contrast with branches in this respect.

Fenestrules are mostly one-and-a-half times to twice the width of branches. Shapes vary, but are commonly rectangular with a width: length ratio of 1 : 2 to 1 : 3. Long sides of fenestrules may be indented by projecting zooecial apertures and show a characteristic beaded or scalloped pattern. This feature is less noticeable on the reverse side.

Zooecial apertures are circular or tear-shaped, with the wider end distally There are three to four opposite each fenestrule and one is always situated centrally in the angle of each bifurcation. All apertures bear a peristome, and the species is characterized by the strong development of this feature, apparently as a result of secondary deposition. Stages in the process appear to be:

1. The presence of a low, rim-like peristome round apertures in younger, distal parts of branches.
2. Increase in height of the peristome rim, and development on its outer side of a strong, basin-like lip that projects into the fenestrule. This must have caused the polypide to be directed obliquely 'upward' rather than laterally.
3. A general thickening and heightening of the peristome to form a collar-like structure that attains, on the inner side, a greater height than the median keel. At this stage the latter has the appearance of a thread lying between alternating peristome rims projecting above it on either side.
4. Further secondary deposition caused the cowl-like peristome to bulge into the fenestrule. The terminal aperture may be constricted or even sealed altogether. The increasing size is manifested as a distinct bulge on the obverse branch surface, and alternating bulges may coalesce across the mid-line so that the keel is obscured or lost, though the tips of carinal nodes remain visible. The obverse now has a knobbly appearance due to the alternating peristomial inflations, and the appearance differs greatly from that of a young branch.

It is notable that in this species secondary skeletal material accumulated principally on the reverse of branches and around zooecial apertures, not along the keel as in many other forms. This leads to a distinctive appearance in heavily encrusted parts of colonies.

Zooecial chambers are triangular or trapezoid in plan, mostly the latter. Average dimensions of twenty chamber bases were: length of longer side, 0·17 mm; length of shorter side, 0·07 mm; width between these, 0·15 mm. A single perfectly preserved chamber filling had the appearance of a pear or rounded flask, with trapezoid base and the aperture at the termination of a short neck.

The slender median keel bears small carinal nodes spaced rather widely apart. A few specimens also showed an irregular row of small nodes along the mid-line on the reverse surface. These are commonly 0·1–0·22 mm apart and may also be present on dissepiments. Such nodes are not uniformly distributed and may be present in one part of a specimen but not in another. From some fragments they are altogether absent. A few large spinose processes of the kind that appear to have lent support to colonies or assisted in their attachment were also observed. They are uncommon and of relatively small size.

Discussion. Features that characterize this species are the open-textured meshwork, lax mode of growth and the zooecial apertures that commonly protrude into fenestrules due to the presence of inflated peristomes. These seem to be developed as a result of excessive localized secondary secretion, but the appearance is reminiscent of peristomial ovicells in certain cheilostomes, and the possibility that the peculiar shape was associated with a reproductive function cannot be disregarded.

The specimens correspond in all respects with *Fenestella subspeciosa* Shulga-Nesterenko 1955, from the Upper Carboniferous (Gzhelian) of Russia, and are assigned to that species. That author's account includes mention of circular or pear-shaped apertures with a well developed 'lunarium', and the chamber base-shape in her species is trapezoid or bluntly triangular.

There is also some resemblance to the Australian *F. cerva* Campbell 1961. Meshwork dimensions in that species (formula: 10–12/5½–6//10–14/6–9) are similar to those of the Fermanagh material though the branches are more widely spaced and the fenestrules, therefore, broader. The Australian form also has a high, sharply defined keel, with zooecial apertures in a groove on either side. Peristomes are present, but they are not of the inflated type. These features, together with 'sub-pentagonal' chamber bases and the introduction of a short third row of apertures prior to branch division, distinguish *F. cerva* from the specimens described here.

From *F. praemagna*, the Fermanagh material differs in having narrower branches, protruding zooecial apertures, larger rectangular fenestrules and longer, slimmer dissepiments. Another Russian Upper Carboniferous form, *F. gzhelensis*, is similar in some respects but has wider branches (0·4–0·5 mm) and a rectangular or hemi-hexagonal chamber base.

Fenestella pseudovirgosa Nikiforova

(Pl. 13, figs 1–9)

1860 *Fenestella virgosa* Eichwald: 360, fig. 9a (non fig. 9b).
1938 *Fenestella pseudovirgosa* Nikiforova: 68.

DIAGNOSIS. Strong, fan-shaped colonial meshwork. Branches roughly triangular in cross-section. High median keels bear stout, widely spaced nodes. Zooecial apertures large; chambers mostly triangular.

MATERIAL. More than 140 zoarial fragments of this common and distinctive form were examined. The largest, from the proximal and medial parts of a colony, was 30 × 18 mm. PD.4770–7, PD.5141–57.

Measurements (N = 25):

	A	B	C	D
F.l.	1·40–2·37	1·868	0·179	9·58
F.w.	0·87–1·17	1·004	0·078	7·74
I.ap.s.	0·30–0·39	0·347	0·245	7·05
I.n.s.	0·75–1·57	1·126	1·757	15·61
B.w.	0·37–0·50	0·429	0·033	7·75
Ap.d.	0·12–0·17	0·158	0·015	9·34
Diss.w.	0·15–0·30	0·222	0·032	14·40

Micrometric formula: 8–13/4–7//12–15/2–6.

Apertures per fenestrule.

Range of specimen modes:	4	5	6
Distribution of specimen modes:	10	12	3

Description. The zoarium is a planar, flabellate expansion with variable meshwork texture. Branches and dissepiments are much thickened proximally by secondary encrustation, and fenestrules correspondingly reduced in size. Distally, branches are more widely spaced and thinner, with larger fenestrules.

Branches are relatively stout with an approximately triangular cross-section. Their sides slope steeply from a strong median keel on the obverse, while the reverse is broadly rounded. In proximal parts the keel may have a pronounced rope-like aspect due to the selective deposition of secondary schlerenchyma. Lateral thickening of this kind may cause it to overhang zooecial apertures. Secondary material may also thickly coat the reverse and lower flanks of branches so that the apertures come to lie in a groove parallel with the keel and below it on each side. Continued secretion of secondary schlerenchyma near the growth origin may result in the occlusion of apertures, which are sealed by a convex cap. This gives branch margins a beaded appearance that is particularly evident where branches are steep-sided.

The reverse surface commonly shows longitudinal striae, and in well-preserved specimens the fine ridges may bear rows of minute papillae. These are about 0·01 mm in diameter and spaced 0·03–0·06 mm apart. Similar grooves and ridges with papillae are seen on the obverse, but there 'striae' are not parallel to the branch axis but sinuous, following the contour of the surface. Ridges with rows of papillae may be very evident on the keel and under side where these are thickly coated with secondary material.

Dissepiments are straight and bar-like, though in older parts of zoaria they may flare considerably at either end. They are depressed below branch level on both sides, have a circular section, and are commonly about half as wide as branches, though there is much variation. Dissepiments may show grooves and ridges parallel to their length. These merge with corresponding structures on adjacent branches and also carry rows of papillae.

The size and shape of fenestrules varies greatly, the commonest shape being an elongate rectangle with rounded extremities. Proximally, fenestrules may be elongate-oval and of reduced size, due to the relatively close spacing of branches encrusted with secondary tissue. Fenestrule margins are mostly straight, but the long sides may show a beaded pattern where apertures are sealed by conical 'caps', or well-developed peristomes are present.

Zooecial apertures are large, circular and spaced about one diameter apart. They are not regularly situated with respect to dissepiments. Plain, narrow peristomes may be present and, particularly on steep-sided branches, these may be accentuated on the outer side so as to project slightly into fenestrules.

The chamber base-shape is mostly triangular, average measurements of twenty being: length parallel to branch, 0·3 mm; width (perpendicular to branch), 0·16 mm. Some triangles are longer and narrower (0·35 mm × 0·14 mm), while others are shorter but wider (0·25 mm × 0·17 mm). In a few cases the apex of the triangle is truncated, to give a trapezoid shape (long side: 0·28 mm; short side: 0·09 mm;

width: 0·17 mm). Walls of zooecial chambers are perpendicular to the base-plane throughout their height.

The median keel bears a row of strong nodes or spines. These are in all cases truncated by breakage but may be up to 0·9 mm high and 0·15 mm in diameter at the base. Small, irregularly distributed nodes are present on the reverse, generally along the mid-line of a branch or close to it. Average space between ten pairs of nodes is 0·82 mm, but there is much variation. The diameter of the nodes is from 0·07 mm to 0·12 mm, and many are no higher than wide, though a few rise to 0·8 mm.

Stout supporting spines may originate from obverse or reverse, or laterally as branch continuations. If well-preserved they show parallel ridges and striae which merge with those of the parent branch; the ridges commonly show rows of papillae of the kind already mentioned. On the obverse such spines grow from positions where a carinal node might otherwise have been expected. They are always broken distally, but may be up to 2 mm long, with a basal diameter of 0·27 mm. Although much longer than carinal nodes, the structure appears to be identical, and it is probable that the spines resulted from the continued growth of certain nodes. Similar spines on the reverse are longer and stouter: up to 6 mm in length and 0·7 mm in basal diameter. Some well-preserved specimens show a radiate internal structure reminiscent of the septa of a rugose coral. Lateral spines may develop either as sterile continuations of branches, or at right angles to the branch axis, in the position of a dissepiment. These spines are up to 7 mm long and 0·52 mm in basal diameter.

Discussion. The radiate cross-section of spinose processes mentioned above is commonly seen in good specimens of these structures. It may occur in conjunction with the concentric pattern of secondary laminae, and the parallel with septa and dissepiments in rugose corals is then particularly evident. The radial elements appear to be silicified skeletal rods which originated from the primary core of a spine and passed through the laminated secondary tissue to the periphery.

These specimens appear to be identical with *Fenestella pseudovirgosa* Nikiforova 1938, from the Russian Upper Carboniferous. This species is not well illustrated (1938 : pl. X, figs 6 and 7), but the Fermanagh material appears to agree in all respects with the comprehensive description (Ibid. : 68–70, 228) of the Russian species, to which it is therefore assigned. There is also a strong resemblance to *F. regalis* Ulrich 1890, from the Keokuk (probably early Visean) of Kentucky, but this has very wide branches (average 0·7 mm against 0·43 mm) and hemi-hexagonal to rectangular zooecial chamber bases. Koenig (1958 : 134) assigned specimens with an average branch width of about 0·4 mm to *F. regalis*, which might seem to justify the inclusion of the present material also, but the important discrepancy of chamber base-shape remains. *F. eichwaldi* Stuckenberg 1895, is another species to which there appears to be a strong similarity, though there are differences relating to branch width (0·56–0·67 mm compared with 0·37–0·5 mm) and apertural size (diameter 0·2 mm). Also fenestrules and dissepiments are wider in the Russian form. The most important difference, however, affects zooecial chamber plan, that of *F. eichwaldi* being hemi-hexagonal to rectangular. It seems possible that this species is conspecific with *F. regalis*, and perhaps the same applies to *F. crockfordae* Campbell 1961, from the Australian Kuttung (Upper Carboniferous).

Campbell's form is much like the Fermanagh one but differs in having an 'irregularly pentagonal' chamber base and a short third row of apertures prior to branch divisions.

Fenestella cf. ***albida*** Hall

(Pl. 14, figs 1–6)

MATERIAL. This is a fairly common form and more than 80 specimens were examined. They were almost all fragments from the medial part of colonies. The largest measured 34 × 12 mm. PD.4778–85, PD.5158–74.

Measurements (N = 25):

	A	B	C	D
F.l.	1·52–2·15	1·830	0·192	10·50
F.w.	0·75–1·00	0·869	0·064	7·42
I.ap.s.	0·32–0·40	0·350	0·187	5·36
I.n.s.	0·62–0·92	0·742	0·079	10·64
B.w.	0·25–0·30	0·272	0·019	6·89
Ap.d.	0·12–0·15	0·138	0·010	7·22
Diss.w.	0·15–0·22	0·170	0·020	11·76

Micrometric formula: 10–15/4–6//12–16/5–8.

Apertures per fenestrule.

Range of specimen modes:	4	5	6	7
Distribution of specimen modes:	7	12	6	0

DESCRIPTION. The fragmentary specimens suggest that complete zoaria were fan-shaped expansions with a lax, open meshwork. Branches are relatively thin, and sinuous rather than rigid. There is a distinct, thread-like median keel, on either side of which the branch surface slopes steeply away to the lateral margins. These are gently sinuous or scalloped, due to the presence of a slight inflation below each zooecial aperture. The obverse is strongly ridged and grooved between apertures, and the broadly rounded reverse bears fine longitudinal striae. There may also be a row of small tubercles along the reverse mid-line. Branch divisions are common in the proximal region, and some fragments show zones where adjacent branches divided simultaneously. This contributed to the rapid attainment of the flabelliform shape of colonies. At bifurcations there is a characteristic wish-bone pattern, owing to an initially wide divergence angle between each new pair of branches, which then converge slightly before following a parallel course.

Dissepiments are thin, irregularly spaced and slightly depressed below branch level on both sides. There is no marked increase in width at extremities, and transverse sections are oval, the long axis being parallel with the branch height. Owing to the sinuous growth habit of branches the length of dissepiments is variable: some are slender and bar-like, while others are relatively short and stout.

Fenestrules are large, with much variation in size and shape. Most are elongate rectangles with rounded extremities and beaded branch margins. The ratio of width to length varies between 1 : 1½ and 1 : 4, depending on the spacing of dissepiments.

Zooecial apertures are prominent, with a circular, oval or (most commonly) pear-shape. In the last case the large end is distal, and the long axis slightly oblique. Thin rim- or collar-like peristomes are commonly present and tend to be strongly developed on the outer side. These, in conjunction with localized inflations of the branch margin, may form hood- or lunarium-like structures around the distal ends of apertures. A combination of the features mentioned commonly gives branches a distinctive chain-like appearance on the obverse.

Zooecial chamber bases are triangular or trapezoid. Average dimensions of seven triangles were: length (parallel to branch margin) and width (perpendicular to length), both 0·2 mm. In trapezoid chambers the average measurements of five were: longest side, 0·22 mm; shortest side, 0·09 mm; perpendicular width between these, 0·17 mm.

Carinal nodes are widely spaced and insignificant rarely exceeding 0·12 mm in height. Nevertheless they may show an unusual development. In one specimen, typical of several, a thick carinal node attained a height of 0·32 mm (about the same as that of a branch), then turned abruptly through 90° into parallelism with the colonial meshwork. As it grew onward in this direction a number of lateral processes were given off, also parallel with the mesh. The longest of these united with the distal end of another large carinal node situated two branches away from the first, so that the beginnings of a superstructure were formed. This was originally more extensive than at present, for other lateral processes, also showing signs of former union with carinal nodes, are broken off short.

In addition to carinal nodes there are small tubercles on the reverse mid-lines of branches and dissepiments. These are mostly uniserial but the arrangement tends to be irregular, and may be biserial for short distances. Node bases are about 0·25 mm in diameter and spaced about 0·1–0·15 mm apart.

One small specimen, from the proximal part of a colony, showed a number of lateral supporting spines attached to the reverse of another fenestrate fragment. The spines are short and grew as branch continuations, or from the position of dissepiments. If the second fragment lay reverse-up on the sea floor, the spine-bearing specimen must have rested on its side in a plane perpendicular to the substratum. Possibly the growth axis was originally upward but the small colony was displaced for some reason.

Discussion. It is probable that this is the form described by Phillips (1836 : 199) as *Retepora undulata*. His description is too brief for this to be certain, but it nevertheless includes some of the diagnostic features, such as the presence of thin branches, large fenestrules of variable size and shape, and prominent zooecial apertures. The illustrations (pl. 1, figs 16–18) are also insufficient by present standards, but they succeed in calling attention to salient features also shown by the Fermanagh specimens Figure 16 is drawn to natural size (with which the present material corresponds well) and illustrates the open texture, relatively thin branches and dissepiments, and the fact that the latter may be oblique. Figure 17 shows the striated nature of the reverse side, with scalloped branch margins and straight, bar-like dissepiments, while in Fig. 18 the distinctive shape of the zooecial apertures is apparent. These similarities are enough for the writer to consider that the form discussed here is that described by Phillips. In spite of this it seems inadvisable to refer the material to his species, for the type specimens are lost and the existing descriptions inadequate. Miller (1961 : 225) declared *Retepora undutala* Phillips a *nomen dubium* for these reasons, and there is little hope of reviving the species by describing a neotype, owing to the lack of information about collecting localities (merely given as 'Harrogate, Bolland, Hawes' by Phillips).

Fortunately the species, or a form very close to it, was described from America under the name *Fenestella albida* Hall 1886. It was collected from the Waverly formation (Mississippian) of Ohio. The Fermanagh specimens correspond well with Hall's description and illustrations except that the apertures are more widely spaced (20 in 5 mm according to Hall), carinal nodes are slightly closer (4 per 5 mm in the American form) and branches a little wider (0·25–0·3 mm against 0·18–0·25 mm). However, Koenig (1958 : 133) assigned to *F. albida* specimens with the formula: 15–16/6//16–17/4, and these had rather more widely spaced apertures than Hall's material. The spacing of apertures presents the only important discrepancy between the Irish and American forms, but in view of the diagnostic importance attached to this feature it seems best not to make a firm allocation to Hall's species.

Fenestella oblongata Koenig, 1958

(Pl. 14, figs 7–8; Pl. 15, figs 1–4)

1958 *Fenestella oblongata* Koenig; 132.
1962 *Fenestella oblongata* Koenig; Miller; 123.

Diagnosis. Cylindroid branches lacking a median keel are united by bar-like dissepiments which may be irregularly spaced. Apertures large; placed well away from the branch mid-line, along which occur prominent, widely-spaced nodes.

Material. Fifty-four fragmentary specimens were examined, the largest being 19 × 24 mm. PD.4786–93, PD.5175–86.

Measurements (N = 20):

	A	B	C	D
F.l.	1·67–2·62	2·054	2·200	10·74
F.w.	0·77–1·10	0·899	0·076	8·51
I.ap.s.	0·31–0·37	0·338	0·020	5·84
I.n.s.	0·67–1·25	1·032	0·147	14·28
B.w.	0·35–0·42	0·379	0·017	4·62
Ap.d.	0·10–0·13	0·120	0·010	8·33
Diss.w.	0·17–0·25	0·202	0·021	10·25

Micrometric formula: 10–13/3–6//13–16/4–7.

Apertures per fenestrule.

Range of specimen modes:	5	6	7
Distribution of specimen modes:	8	11	1

Description. On the evidence of specimens examined it is probable that complete zoaria were slightly undulating or foliaceous, fan-shaped expansions a few centimetres across. Due to the gently sinuous growth habit of branches and somewhat irregular spacing of dissepiments, the meshwork commonly has a lax appearance.

Branches are stout, with an approximately circular cross-section. There is no median keel, but along the obverse mid-line is a row of prominent, though widely spaced nodes. The branch surface on both sides is gently convex and bears fine, closely-spaced longitudinal striae. These are straight and parallel on the reverse, but sinuous and less well-marked on the obverse.

Dissepiments are strong and bar-like, not expanding much at the ends. They are about half the branch width and may bear longitudinal ridges and grooves. Dissepiments commonly show irregular spacing and in a few cases two occur close together, as if accidental duplication had taken place. They are quite strongly depressed below the branch crest on the obverse, but not so strongly on the under side.

Fenestrules are mostly rectangular, but there is much variation, due to the sinuous growth of branches and irregular spacing of dissepiments. Shapes vary from broad to narrow rectangles, and may also be elongate-hexagonal or elliptical. The ratio of width to length is between 1 : 2 and 1 : 5. Long sides are mostly straight but may have a scalloped pattern due to projecting apertures.

Circular zooecial apertures are in two rows, placed well out towards branch margins. They are relatively large, and commonly have thin, rim-like peristomes. In some cases the flank of a branch immediately below each aperture is slightly distended and the aperture itself (slightly larger than normal) projects into the fenestrule. This development may be carried a stage further so that the swelling affects not only the outer side, but the whole branch surface around an aperture. The latter is then situated on a localized inflation of the branch margin looking rather like an inverted tea-cup. Such apertures are larger than usual and this appears to be an original feature, as the rims are undamaged. It is possible that the swellings bearing these enlarged apertures had a reproductive function of some kind.

Zooecial chambers have a triangular or trapezoid base-shape. Average dimensions of six triangles were: length, 0·32 mm; width to apex, 0·2 mm. Eight trapezoid shapes showed the following averages: longest side, 0·27 mm; shortest side, 0·09 mm; perpendicular width between these, 0·22 mm. The transverse walls (those not parallel with the branch margin) of chambers are steeply inclined towards the growth origin.

Large 'carinal' nodes are widely spaced along the obverse mid-line, each rising directly from the convex branch surface, as there is no median keel. One of them, which appears to be complete, is 0·25 mm high and 0·2 × 0·12 mm at the base. Many have been destroyed, leaving only elliptical base scars (long axes parallel with branch) to indicate their former presence. Between each pair of nodes there is a series of tiny pustules or tubercles, each about 0·02 mm in diameter, and spaced about 0·12 mm apart. They are mostly uniserial but the arrangement tends to be ragged and may locally be biserial.

On the reverse there is an irregular row of small nodes along, or close to the mid-line. These are up to 0·12 mm high, with about 0·1–0·2 mm between adjacent node centres. Elliptical base scars are about 0·17 × 0·12 mm. There is a good deal of variation in the size, spacing and distribution of these structures. Some specimens have many, others few.

A few strong supporting spines arise from the meshwork on the obverse and reverse surfaces (one from the latter is 8 mm long), and also laterally as branch continuations (one extended for 6 mm beyond the last zooecial aperture). In the latter kind, longitudinal striae are uniformly developed on the exterior of the spine immediately beyond the last apertures. The same thing has been noted in other species and confirms that these structures are potentially present on the obverse of branches, though commonly obscured by apertures, keel and carinal nodes. One lateral spine was connected to an adjacent branch by normal dissepiments, thus emphasizing the branch-like characteristics of these structures. Some stout spines that are truncated proximally showed good transverse sections with radiate structure in combination with concentric laminae, resulting in a pattern like that of a spider's web.

DISCUSSION. This form shows a close correspondence with *F. oblongata* Koenig 1958, from the Chouteau Group (probably Tournaisian) of Missouri. The median keel seems to be even less evident in the Irish material than in Koenig's specimens, and the reverse side of branches is not noticeably subangular, as mentioned in his description. Also, dissepiments in the Fermanagh material are somewhat wider (0·175–0·25 mm compared with an average width of only 0·11 mm). However, none of these differences is important enough to warrant separation from Keonig's species, with which in other respects there is the closest agreement. *F. oblongata* has previously been identified in Ireland by Miller (1962 : 123) on the basis of specimens from the Tournaisian of Hook Head, Wexford. These had the formula: 8–14/5–7//15–20/6–8. Neither Koenig nor Miller gave any account of the shape of the zooecial chamber.

Fenestella cf. ***delicatula*** Ulrich

(Pl. 15, figs 5–8; Pl. 16, figs 1–3)

MATERIAL. More than sixty zoarial fragments of this distinctive form were examined, the largest being 19 × 22 mm. PD.4794–801, PD.5187–203.

Measurements (N = 25):

	A	B	C	D
F.l.	1·55–2·60	2·177	0·207	9·50
F.w.	0·72–1·02	0·844	0·080	9·50
I.ap.s.	0·25–0·34	0·295	0·021	7·27
I.n.s.	0·47–1·52	0·848	0·316	37·18
B.w.	0·22–0·27	0·247	0·018	7·19
Ap.d.	0·09–0·12	0·106	0·009	8·25
Diss.w.	0·12–0·22	0·169	0·025	14·64

Micrometric formula: 10–12/3–6//13–17/3–10.

Apertures per fenestrule.

Range of specimen modes:	4	5	6	7	8
Distribution of specimen modes:	1	3	11	8	2

Description. The complete zoarium appears to have been a medium sized, gently undulose, fan-shaped expansion. One specimen with a basal holdfast clearly indicates that colonies grew in an erect position. The distinctive open-textured meshwork is composed of thin, widely-spaced branches and even thinner dissepiments, bounding relatively large fenestrules. Branches divide repeatedly in the proximal region, where they may have a lax pattern of growth, and diverge appreciably to right and left of the colonial origin. In medial and distal parts they tend to be straight and more or less parallel. Branches are steep-sided on the obverse, with a clear median crest that may be thickened and rendered more prominent by secondary skeletal accretion. In extreme cases the keel assumes a rope-like appearance and slightly overhangs the zooecial apertures beneath. The reverse is smoothly rounded but may show fine, closely-spaced, longitudinal striae. In some specimens these are also visible on the obverse, where they are less regular and tend to have sinuous courses, curving round zooecial apertures. There is no noticeable change in branch width before or after bifurcation.

Dissepiments are straight, thin (commonly little more than half the branch width) and distantly placed. They do not expand much at the union with branches, so that fenestrules have good rectangular shapes with sharp angles. Dissepiments are strongly depressed on the upper surface, but flush with branch level on the reverse.

Proximally, fenestrule shapes are variable and commonly irregular, due to the divergent branch pattern and high incidence of bifurcation. In the medial and distal parts they are mostly rectangular, with a length to width ratio of about two or three to one. The long sides of fenestrules are straight and not indented by projecting zooecial apertures.

The relatively small zooecial apertures are spaced one-and-a-half to two diameters apart, and from the steeply inclined sides of branches they face almost directly into fenestrules. The position of apertures in relation to fenestrules and dissepiments is not fully stabilized, though there is commonly an aperture opposite each branch-dissepiment junction, and one is always centrally placed in the angle where branches divide. Peristomes are present on a few specimens as plain, low, collar-like structures. They appear to have developed as a consequence of secondary accretion round apertures, the peristomial shape being determined by the path of polypides in extrusion and retraction. Zooecial chambers have a trapezoid base plan, average dimensions of eleven being: longest side, 0·17 mm; shortest side, 0·07 mm; perpendicular width between these, 0·15 mm.

The median keel carries a single row of insignificant nodes clearly seen in only a few specimens. Their spacing shows much variation but is fairly constant within a fragment. Where nodes are placed far apart there may be a number of small tubercles between each pair and, since carinal nodes are not large, this adds to the difficulty of obtaining a correct count. Shulga-Nesterenko has described similar features (e.g. 1951 : 23 and text-fig. 2a) and commented on the difficulty that may arise in differentiating between true carinal nodes and intervening tubercles. Clearly it would be inadvisable to use carinal nodes for discriminatory purposes in such forms, and counts need to be accepted with caution.

A few specimens have an irregular row of small nodes along the reverse mid-line.

Spacing of these approximates to that of carinal nodes on the same branch. The nodal diameter is commonly about 0·07 mm and the distance between pairs from 0·37 to 0·75 mm.

A few relatively small supporting spines are present on the obverse and reverse of the meshwork. Lateral processes arising as continuations of branches are common and extend for up to 4 mm beyond the last zooecial aperture. Truncated ends of these show a thick zone of closely-spaced concentric secondary laminae traversed by skeletal rods. The latter radiate from an axial canal with toothed circumference, originally occupied by primary skeleton.

Discussion. The slender meshwork and large fenestrules of this form at once suggest Ulrich's (1890 : 549) *Fenestella delicatula* from the Coal Measures of Illinois (probably late Namurian—Westphalian). There is good agreement with the description of that species, in which Ulrich referred to the strong keel with 'occasional very small nodes', features that also characterize the present material. Although zooecial apertures in his specimens were small and widely spaced, they differed from those of the Fermanagh form in having prominent peristomes that projected into fenestrules. The illustration (1890 : pl. LII, fig. 2) clearly shows this feature, and the beaded appearance of branch margins is quite different from that of the Irish specimens. This is apparently the only discrepancy and in view of the identity in all other respects the specimens are provisionally referred to *F. delicatula*. In examining the etched residues it was found that differences of peristome development were common between members of a species.

Another form to which the present material shows a close resemblance is *F. tenuivirgata*, Shulga-Nesterenko, 1951, from the Russian Lower Carboniferous. This has thinner branches and dissepiments, but in other respects the two appear to be identical. Ulrich gave no information about the zooecial chamber of *F. delicatula*, but in *F. tenuivirgata* it is triangular or trapezoid. There do not appear to be any discrepancies between these two species that could not reasonably be attributed to intra-specific variation and they are here considered to be conspecific.

Fenestella polyporata (Phillips)

(Pl. 16, figs 4–8; Pl. 17, fig. 1)

1836 *Retepora polyporata* Phillips; 199.
1843 *Fenestella polyporata* Phillips; Portlock; 323.
1844 *Fenestella multiporata* M'Coy; 203.
1879 *Fenestella polyporata* Phillips, Shrubsole; 280.
1881 *Fenestella polyporata* Phillips; Shrubsole; 185.
1926 *Fenestella polyporata* Phillips; Nikiforova; 179.
1927 *Fenestella* aff. *polyporata* Phillips; Nikiforova; 251.
1933a *Fenestella polyporata* Phillips; Nikiforova; 23.
1935 *Fenestella* ex. gr. *polyporata* Phillips; Nekhoroshev; 69.
1938 *Fenestella* aff. *polyporata* Phillips; Demanet; 44.
1948 *Fenestella* cf. *polyporata* Phillips; Oakley; 88.
1951 *Fenestella polyporata* Phillips; Shulga-Nesterenko; 59.
1956 *Fenestella* cf. *polyporata* Phillips; Nekhoroshev; 149.
1961 *Fenestella polyporata* Phillips; Miller; 233.

Diagnosis. Open-textured, fan-shaped colonial meshwork with large rectangular fenestrules. Mostly eight or nine zooecial apertures per fenestrule length. Tall, slender carinal nodes are widely spaced.

Material. This species is common in the etched residues from Carrick Lough. Over a hundred fragments were examined, representing all parts of zoaria. The largest measured 22 × 17 mm. PD.4802–7, PD.5204–18.

Measurements (N = 21):

	A	B	C	D
F.l.	2·30–3·80	3·067	0·339	11·05
F.w.	1·00–1·20	1·105	0·057	5·16
I.ap.s.	0·30–0·35	0·312	0·012	3·93
I.n.s.	0·70–1·25	1·074	0·131	12·22
B.w.	0·32–0·42	0·376	0·021	5·51
Ap.d.	0·11–0·14	0·121	0·007	5·35
Diss.w.	0·17–0·25	0·199	0·020	10·19

Micrometric formula: 9–19/3–4//14–17/4–6.

Apertures per fenestrule.

Range of specimen modes.	7	8	9	10
Distribution of specimen modes:	2	6	8	5

Description. The zoarium was a fan-shaped expansion, probably between 4 and 8 cm wide. The coarse meshwork of straight branches and bar-like dissepiments has a rigid appearance.

Branches are of moderate width with clear median crests from which obverse surfaces slope outward to the fenestrules. The underside is rounded and bears fine, closely-spaced longitudinal striae.

Dissepiments are thin, straight, fairly regularly spaced and do not expand greatly at the ends. They are strongly depressed below branch crests on the obverse, but only slightly on the reverse. Fragments from the distal parts of colonies have slender dissepiments, and in a few cases the junction between the initial 'bud-projections' from adjacent branches may be seen. This appears as a slight nick or discontinuity in the surface pattern of longitudinal grooves and ridges. It may be situated mid-way along the dissepiment or be asymmetrical. In one case the union was not quite complete, and the ends of two pairs of ridges, though in contact, are still recognizably lobate.

Fenestrules are rectangular with good shapes, due to the straight-sided branches and bar-like dissepiments. A width to length ratio of about one to three is common.

Zooecial apertures are circular, slightly ovoid (with long axis parallel to branch length) or kidney-shaped. They face obliquely 'upward' and away from the branch surface. Low, plain, rim-like peristomes may be present and tend to be most pronounced on the outer sides. In a few specimens small distensions of the branch margin below each aperture cause peristomes to project slightly into fenestrules.

Many fragments have a short third row of apertures immediately before branch divisions. The additional row commonly consists of only one or two apertures, but may contain three or four, and in one case an extra row of ten apertures extended for a distance of one-and-a-half fenestrules. Mostly the appearance of a third row is soon followed by bifurcation, but in some cases the extra row aborts after a short distance and the branch, having widened slightly to accommodate it, returns to its normal width.

A few specimens from the proximal parts of colonies show apertures sealed by a translucent, plate-like deposit. Closer examination shows that this is not an operculum-like structure, but a continuation of the secondary skeleton over the aperture. The translucent appearance is due to the thin skeletal layer sealing a hollow chamber beneath. In some cases the seal is incomplete, being pierced by a small central orifice, and the appearance is then reminiscent of 'blind cells' in the Cheilostomata (e.g. Bassler 1953 : G156). It seems likely that this represents a late stage of the sealing process at which the moribund zooecium may still have functioned weakly.

The zooecial chamber has a hemi-hexagonal base 0·33 mm (max. length) by 0·15 mm (max. width). The short lateral walls are inclined, and the hemi-hexagonal shape relates only to the proximal end of the zooecium. From this the chamber extends distally as an inclined tubular structure terminating at the aperture. The average overall length of nine zooecia was 0·52 mm.

Well-preserved carinal nodes are tall, slender columns up to 0·6 mm high (average height of ten branches: 0·32 mm). In a few cases the distal ends showed the rounded, lobate extremities of secondary longitudinal ridges surrounding an axial tube (Tavener-Smith 1969 : 301, text-fig. 7c). The latter was originally occupied by the primary skeleton, and the lobed distal ends indicate that the nodes were still growing. Many carinal nodes are missing, their former positions being marked only by slit-like node-bases parallel with the branch axis.

A few longer spines rise from the obverse and reverse sides of specimens. One of these, with a length of more than 3 mm, is only 0·4 mm away from the undamaged tip of a branch. The latter shows little secondary encrustation and if, as seems probable, it was still growing, the length of the spine testifies to the rapidity with which such structures could develop.

Another spine, from the obverse of a specimen, branches at its extremity into a number of processes radiating in a plane almost normal to that of the main shaft. One of these grew strongly, but the others are short and little more than stumps. Outgrowths of this kind are strongly reminiscent of the form-genus *Palaeocoryne*, supposed by Ferguson (1963) to represent separate organisms growing in close association with *Fenestella*.

DISCUSSION. The presence of a third row of zooecial apertures proximally to branch divisions indicates a delay between the dual budding of a zooecium, that produced the extra zoids, and the bifurcation that provided more branch space to accommodate them. It commonly happens that on the appearance of extra apertures the normal alternating biserial pattern is lost and a confused arrangement results, only to be resolved when bifurcation takes place. In other examples one series of apertures manages to maintain the usual biserial order, while the other is displaced to one side, usually with a raggedly uniserial appearance. Although this situation is commonly followed by an orthodox symmetrical bifurcation, in some cases the biserial apertures continue into a stouter branch than the other. Where inequality of this kind is evident it may also happen that the stronger branch continues the original axis of growth, while the other is deflected at an angle. Asymmetry of this kind is the rule in *Ptiloporella* and distinguishes that genus from *Fenestella* which was, no doubt, the parent stock.

The specimens are assigned to *F. polyporata* (Phillips) 1836, though there are discrepancies with some of the measurements given by Miller (1961 : 233) in re-describing that species. In general the meshwork of the Fermanagh material is a little coarser than in the two specimens used by Miller: fenestrules are slightly longer, branches and dissepiments are wider. Measurements given by Nikiforova (1926 : 177) and Shulga-Nesterenko (1951 : 30–31) for the same species bridge this gap to a large extent and seem to justify the inclusion of the present material. The relevant data are:

	F.l.	F.w.	B.w.	Diss.w.
Carrick Lough	2·12–3·55	0·67–0·77	0·32–0·42	0·17–0·25
Miller, 1961	2·05–2·25	0·45–0·60	0·22–0·33	0·11–0·16
Shulga-N., 1951	1·90	0·80	0·35	0·10–0·15
Nikiforova, 1926	2·00–2·50	0·62–0·75	0·30–0·37	0·12

The unusual width of dissepiments in the present material might be due to the fact that many of the specimens are old and encrusted. Local ecological factors, requiring for some reason an unusually strong framework, may also have had some influence. Apart from these dimensions there is complete agreement with Miller's description.

Fenestella irregularis Nekhoroshev

(Pl. 17, figs 2–7)

1932 *Fenestella irregularis* Nekhoroshev; 56.

Diagnosis. Differs from *F. polyporata* in having slightly coarser meshwork of wider branches with bi-convex cross-section. Peristomes more strongly developed and commonly indent fenestrules. Zooecial tubes have hemisepta.

Material. This extremely coarse-meshed form is common in the residues, and about a hundred fragments were examined. The largest of these measured 28 × 15 mm. PD.4808–13, PD.5219–37.

Measurements (N = 25):

	A	B	C	D
F.l.	2·70–3·70	3·184	0·287	9·01
F.w.	1·00–1·50	1·200	0·126	10·50
I.ap.s.	0·27–0·37	0·314	0·014	4·54
I.n.s.	1·00–1·50	1·313	0·122	10·10
B.w.	0·37–0·47	0·425	0·031	7·41
Ap.d.	0·01–0·14	0·122	0·006	5·33
Diss.w.	0·17–0·30	2·330	0·032	13·84

Micrometric formula: 7–10/2–4//15–18/3–5.

Apertures per fenestrule.

Range of specimen modes:	7	8	9	10	11	12
Distribution of specimen modes:	1	7	10	5	2	2

Description. The complete zoarium appears to have been a large, slightly undulose, fan-shaped expansion. In one specimen a basal holdfast is attached to the reverse of another fenestrate fragment, and suggests that the growth habit was erect or partly erect, from a substratum of organic debris.

Branches are gently sinuous, giving the meshwork a rather lax appearance. They are stout, with a roughly circular cross-section. Along the obverse mid-line is a low, thread-like keel on either side of which the surface slopes gently to the branch margin. On the reverse are fine, closely-spaced longitudinal striae, and these are also visible to a lesser extent on the flanks and obverse, where they are sinuous rather than straight.

Dissepiments are bar-like and notably thinner than branches. They show little increase in width at their ends, so that fenestrules have sharp, angular extremities. Dissepiments are slightly depressed below branch level on both sides and commonly bear fine longitudinal ridges and striae. In the older parts of zoaria they may be considerably thickened by secondary encrustation.

The large, distinctive fenestrules are mostly rectangular though, due to the sinuosity of branches, they may be elongate-hexagonal. In some specimens the long sides have a beaded appearance caused by the lateral projection of zooecial apertures from branches.

Two rows of alternating apertures are placed close to branch margins and away from the keel. They are mostly circular, though some are elliptical, with the long axis transversely across the branch and others (in the proximal region) kidney-shaped. Prominent collar-like peristomes are commonly present and may give apertures a protruberant appearance. They are particularly well developed on the outer side and may project slightly beyond the branch margin.

The zooecium is basically an elongate tube with a terminal aperture. A distinct oblique septum about one-third of the way from the proximal end separates off a slightly distended, bag-like chamber. This has a more or less hemi-hexagonal plan and short lateral walls that are inclined proximally. The septum is situated further from the aperture than is usual with hemisepta, but if it is a structure of that kind it must be described as 'inferior', being apparently of dorsal origin. Alternatively it may be a diaphragm of the type reported by Miller (1962 : 543) in the Silurian genus *Archaeofenestella*. Beyond the septum the zooecium continues as a stout tube inclined at about 40° to the base of the branch. It is moulded to rest on the proximal chamber of the succeeding zooecium, and against that of its neighbour in the next row. At the base of the vestibule, where the tube turns sharply towards the branch surface, there is a constriction caused by a shelf-like projection from the ventral side. This appears to be a superior hemiseptum. The average overall length of eight zooecial chambers was 0·47 mm, and the length and width of the same number of proximal chambers averaged 0·175 mm and 0·15 mm respectively.

The hemi-hexagonal to triangular zooecial base plan in this species relates only to the proximal extremity of the tube, and gives no indication of the true zooecial shape. The apparent chamber shape seen in thin sections varies according to the level at which the section is cut, being hemi-hexagonal below and oval to rectangular above.

The thread-like median keel on the obverse of branches bears small, widely separated nodes. These are mostly truncated by breakage, but apparently complete ones may attain a height of 0·5 mm, about equal to that of branches. Node-bases are oval and show slit-like axial cavities. The average dimensions of seven were: length (parallel to branch), 0·375 mm; width, 0·15 mm. Fragments belonging to this species bear an unusual number of adherent organisms (including *Fistulipora*, *Tabulipora*, small gastropods and foraminifera) on the obverse side. Perhaps this is in some way connected with the sparsity and small size of carinal nodes.

Spinose processes may grow from either side of the meshwork, or laterally as branch continuations. In most specimens they are few in number and short, though one fragment carried a slender spine that extended for 6 mm from the obverse mid-line.

Discussion. Comparison of these specimens with those assigned to *F. polyporata* (Phillips) showed statistically significant ($P < 0{\cdot}05$) differences in branch and dissepiment width and internodal distance. Also the keel is more pronounced in the *F. polyporata* specimens, in which branches have a triangular rather than a rounded cross-section. Zooecial tubes in both forms show the same general shape, but those of the *F. polyporata* sample do not exhibit the well-developed septa described above. For these reasons the two forms must be differentiated, in spite of superficial resemblances.

Among coarse-textured species of *Fenestella* the present material is closest to *F. irregularis*, Nekhoroshev 1932, from the Tournaisian of Germany. With the description of this form there is complete agreement, and the specimens are, therefore, referred to it. However, they also bear many resemblances to *F. quadradecimalis* M'Coy 1844, a species originally collected from the 'Carboniferous Upper Limestone' at Black Lion, Co. Cavan, about ten miles from Carrick Lough. From this form, as re-described by Miller (1961 : 231), the specimens differ mainly in having more widely spaced apertures (15–18 in 5 mm and 7–12 per fenestrule, as compared with 21–22 in 5 mm and 10–13 per fenestrule). In fact, the Carrick Lough material and *F. quadradecimalis* may have belonged to the same natural species, but in view of the above discrepancy it is necessary to assign the former to the German species, with which there appears to be complete identity. It is relevant to note that Elias (MS. 1950 : 2) assigned to *F. quadradecimalis* specimens from the Lower Limestone Group of Scotland with the formula: 10/3–3½/17–18/none, and 10–13 apertures per fenestrule. He also mentioned the presence of a strong inferior hemiseptum. His material seems morphologically close to that described here, but his notes are very brief and without illustration, so that it is impossible to be certain.

Another coarse-textured form described by Nekhoroshev (1932) from the German Lower Carboniferous is *F. gracilis*. This differs from the present specimens in having more closely spaced and thinner branches, also the inter-apertural distance is greater. *F. crockfordae* Campbell 1961, from the Kuttung (late Carboniferous) of Australia differs in having more widely spaced and larger zooecial apertures, fewer of these per fenestrule, and a short third row on the proximal side of branch divisions.

Genus ***LEVIFENESTELLA*** Miller, 1961

Diagnosis. Like Fenestella, but lacking carinal nodes and a keel-ridge on the obverse of branches. Instead a single longitudinal thread, or several of these in parallel and placed closely together, form a low median crest.

Type species. *Levifenestella maeve* Miller 1961a : 494. Lower Carboniferous, Ireland.

Levifenestella undecimalis (Shulga-Nesterenko)

(Pl. 17, figs 8–9; Pl. 18, figs 1–5)

1961 *Fenestella undecimalis* Shulga-Nesterenko; 112.

Diagnosis. Coarse-textured *Levifenestella* with strong branches, rather flattened on obverse. Fenestrules elongate-rectangular, usually with eight apertures per fenestrule. Apertures commonly transversely elliptical and placed well away from branch mid-line.

Material. This distinctive form is common and more than eighty fragmentary specimens were examined. They were from the medial and proximal parts of colonies, the largest measuring 39 × 17 mm. PD.4814–20, PD.5238–52.

Measurements (N = 22):

	A	B	C	D
F.l.	2·20–2·30	2·991	0·264	8·83
F.w.	1·00–1·30	1·186	0·980	8·26
I.ap.s.	0·30–0·37	0·336	0·212	6·32
B.w.	0·45–0·57	0·448	0·030	6·19
Ap.d.	0·10–0·13	0·116	0·009	7·72
Diss.w.	0·22–0·35	0·268	0·040	15·00

Micrometric formula: 8–12/3–4//13–16/none.

Apertures per fenestrule.

Range of specimen modes:	6	7	8	9
Distribution of specimen modes:	1	7	12	2

Description. Zoarium a near-planar, fan-shaped expansion with open-textured meshwork of stout branches and thinner, bar-like dissepiments.

Branches are more or less flattened on the obverse, with a gently convex profile; the reverse is broadly rounded. The surface is covered by closely spaced longitudinal striae that are straight and parallel on the reverse but gently sinuous on the obverse, due to deflection around zooecial apertures. Along the obverse mid-line are 2–4 (mostly 3) striae separating narrow longitudinal ridges. These may be strongly developed and form a median strip of distinctive appearance, though an orthodox keel is absent. In some specimens the median strip is slightly raised above branch level and, in the proximal region, it may be accentuated by secondary schlerenchyma and fused into a cord-like crest. This may have a notched profile, so that it is locally discontinuous. Notches are from 0·03–0·05 mm wide and of irregular occurrence. Their presence suggests that the deposition of secondary calcium carbonate along the median line was interrupted from time to time, possibly due to temporarily unfavourable conditions. In other specimens the production of secondary tissue in the proximal region was so great that fenestrules are virtually closed and branches welded into a solid mass.

Dissepiments are slightly depressed below branch level on both sides, and show well developed ridges and striae parallel to their length. They are straight, not flaring greatly at the ends, and commonly show some degree of dorsi-ventral flattening, giving an ovoid cross section. In the proximal region dissepiments may be notably thickened by secondary encrustation.

Fenestrules are mostly elongate rectangles with good shapes, though in older parts of colonies the extremities may be rounded. The width of fenestrules is commonly a little greater than that of branches, and the sides are straight or slightly beaded.

Two alternating rows of zooecial apertures are situated close to branch margins and away from the mid-line. The apertures are circular, transversely elliptical (commonest) or kidney-shaped with the convex side distal. They are relatively small, with plain peristomes that rise slightly above the flattened branch surface but do not, as a rule, project laterally into fenestrules. Prior to bifurcation there is commonly an additional row, up to five apertures long, with three or even four abreast where the branches divide. The arrangement in such situations may be confused, and the appearance suggestive of *Polypora*.

Zooecial chambers mostly have a triangular base, though the development of short lateral walls in some cases gives a hemi-hexagonal outline. Eighteen triangles had an average length (parallel to branch margin) of 0·22 mm; and perpendicular width (to apex) of 0·25 mm. The triangular-based chamber is only the proximal part of the zooecium, however. From its distal end there is a wide tubular extension to the aperture. This is parallel with the branch and inclined at a low angle, the vestibular portion of one zooecium resting on the proximal chamber of the next. The length of the vestibular part is about 0·32 mm, and the total length in the order of 0·55 mm.

Spinose processes arise from obverse and reverse sides of specimens, particularly in the proximal region. Many have extensive secondary thickening at the base and, away from the spine, this extends as skein-like ramifications along the obverse mid-lines of branches and dissepiments. Some laterally directed spines that are continuations of normal branches show a constriction immediately after the last zooecial aperture, so that the spine is thinner than the branch. Longitudinal ridges and grooves, particularly those of the obverse mid-line, are continuous from branch to spine, curving gently at the junction in accordance with the decreased diameter.

One specimen of the proximal part of a zooarium includes the basal holdfast, which is attached to another fenestrate fragment. The colony is supported in an upright position by a number of bar-like spines originating from the basal part of the colony and serving as struts between this and the organic substratum.

Discussion. The appearance of a constriction at the base of certain lateral spines suggests that their development may have been initiated by injury to the branch from which they grew. It is as if a broken branch tip was sealed by an overgrowth of secondary schlerenchyma forming a ‘stump’, and that continued growth from this resulted in the spine. It is not contended that all lateral spines originated in this way, but only that certain cases suggest it.

These specimens lack a true keel and carinal nodes, having instead a striated median strip. They must, therefore, be referred to Miller's (1961b : 47) genus *Levifenestella*. Among described species of this kind only one is similar to the present specimens: *L. undecimalis* (Shulga-Nesterenko) 1941, from the Lower Permian of the southern Urals. The Fermanagh form agrees in every respect with the description of this species, to which it is assigned without hesitation. In view of the age difference between the Irish and Russian specimens it is possible that there is here a case of homoeomorphy, and that the species did not, in fact, persist from Lower Carboniferous to Lower Permian times. Future work may shed more light on this matter.

The specimens also bear many resemblances to the common Lower Carboniferous *Fenestella polyporata* (Phillips) 1836. It was at first thought that they belonged to this species, particularly as the type material came from Florence Court, a few miles from Carrick Lough and at approximately the same horizon. Indeed, it seems likely to the writer that Phillips' specimens (1836 : pl. 1, figs 19 and 20) were identical with the form here described, and differed from that now known as *F. polyporata*. His fig. 20 shows a specimen lacking keel, with a striated obverse surface and bearing two rows of small apertures placed well out towards the branch margin. These features, in combination with the wide branches and slender dissepiments shown in the figure, present a strong resemblance to the form discussed here. However, Phillips' specimens are lost and Miller (1961a : 233) has re-described the species on the basis of a neotype that was itself the holotype of M'Coy's (1844 : 203) *F. multiporata*. Miller considered this name a junior synonym of *F. polyporata*, so that his use of M'Coy's specimen in re-describing the latter was justified. Nevertheless, the writer feels that in reality the two forms may have been distinct. From *F. polyporata*, as re-described by Miller, the Carrick Lough specimens differ in lacking a keel and nodes, also in having much wider branches and dissepiments.

Genus ***MINILYA*** Crockford, 1944

DIAGNOSIS. Morphology as for *Fenestella* with the exception that nodes on the obverse branch surface are biserially arranged. Nodes are regularly disposed so that one corresponds with each zooecial aperture.

TYPE SPECIES. *Minilya duplaris* Crockford 1944. Lower Permian, Western Australia.

DISCUSSION. Crockford's generic diagnosis (1944 : 172) was similar to that given above but also stated that zooecial chamber shapes are triangular. Elias and Condra (1957 : 66) rightly pointed out, however, that no single chamber shape characterizes all forms in which the nodes are biserial.

Minilya plummerae (Moore)

(Pl. 18, figs 6–8; Pl. 19, figs 1–4)

1929 *Fenestella plummerae* Moore; 19.
?1951 *Fenestella praerhomboidea* Shulga-Nesterenko; 99.
1961 *Fenestella ninae* Viskova; 87.

Diagnosis. Fine-textured, geometrically regular meshwork. Fenestrules quadrate or hour-glass shaped. Zooecial apertures at ends of dissepiments and midway between them. Strong peristomes commonly indent fenestrule margins.

Material. This fine-meshed species bears a strong resemblance to *F. ivanovi*, from which it is distinguishable only with care. Both are moderately common in the residues, and about thirty-five small fragments of the present form were examined. The largest measured 14 × 6 mm. PD.4821–7, PD.5253–5.

Measurements (N = 10):

	A	B	C	D
F.l.	0·45–0·50	0·475	0·016	3·31
F.w.	0·45–0·52	0·482	0·025	5·21
I.ap.s.	0·23–0·25	0·250	0·006	2·50
I.n.s. (in 1 row)	0·22–0·25	0·242	0·008	3·42
B.w.	0·20–0·22	0·204	0·008	3·91
Ap.d.	0·06–0·07	0·068	0·005	6·90
Diss.w.	0·10–0·12	0·114	0·007	5·89

Micrometric formula: 19–25/20–22//20–21/19–24 (in 1 row).

There were two zooecial apertures per fenestrule in all specimens examined.

Description. In meshwork characteristics and general appearance this form bears a strong resemblance to *F. ivanovi*. Zoarial shape and size were probably similar to those of that species.

Branches are relatively stout in relation to meshwork texture. They show a tendency to widen progressively for one or two fenestrules before branch division, and are narrower than usual immediately afterwards. On the obverse side is a poorly defined median keel; the reverse is broadly rounded and may show fine longitudinal striae.

Dissepiments are similar to those of *F. ivanovi*, though a little shorter. On the reverse side they are depressed below branch level only slightly, if at all.

Fenestrules are mostly quadrate, with well-rounded extremities, due to the increase in width at the ends of dissepiments. The characteristic 'hour-glass' shape seen in *F. ivanovi* is less strongly developed in this form, though paired indentations are present on the sides of many fenestrules. These are less evident on the reverse than on the obverse. Visual comparison suggests that fenestrules are slightly smaller than in *F. ivanovi*, but measurements fail to confirm this. The appearance of reduced size is an illusion possibly promoted by slightly greater branch width in the specimens discussed here.

The position of zooecial apertures in relation to dissepiments is stabilized, with one at each branch-dissepiment junction and one half way along the intervening fenestrule. In the latter situation apertures may project strongly from the branch margin. Peristomes are more marked than in *F. ivanovi*, and this contributes to a superficial impression (not borne out by measurements) that apertures are smaller in the present species. Zooecial chambers are hemi-hexagonal in plan, the average dimensions of ten being: length parallel to branch axis, 0·2 mm; maximum width, 0·087 mm.

Carinal nodes in this form resemble those of *F. ivanovi* in their size and obscurity, but differ greatly in arrangement. The insignificant nodes are placed closely together in alternating rows, one on each side of the median keel. One node is situated on the inside of each zooecial aperture, and the close association of keel, nodes and apertures gives the obverse of branches a crowded appearance.

There are also nodes on the under sides of branches. These are small, acuminate, and inclined in the distal direction. They are commonly located at branch-dissepiment junctions, but may also occur along the mid-line between these positions. Nodes of this kind are identical in shape and position to those described by the writer (1965: 489) in *Ptilofenestella carrickensis*.

Stout supporting spines originate from the reverse of the meshwork, or laterally as sterile branch continuations. Spines from the reverse are commonly armed with short, recurved barbs arranged in cycles of three around the circumference of the shaft. These barbed spines are a characteristic feature and were not observed in *F. ivanovi*.

DISCUSSION. This form is differentiated from the closely similar *F. ivanovi* by the following:

1. Numerical comparisons of structural data by *t*-tests showed a significant difference ($P < 0{\cdot}05$) of branch width, that of *F. ivanovi* being narrower.
2. Zooecial chamber bases in *F. ivanovi* are triangular, while those of the present specimens are hemi-hexagonal.
3. Carinal nodes in *F. ivanovi* are uniserial, while in this species they are biserial and approximately twice as numerous. This difference is not as obvious as it may seem, for in both forms the nodes are weakly developed.

These specimens appear to be conspecific with Moore's *Fenestella plummerae* from the Pennsylvanian Graham Formation of Texas. Because of the presence of biserial carinal nodes, however, the species must be transferred to *Minilya*. Moore's holotype measured only 4 × 3 mm, but in spite of this the present specimens correspond with his description in almost every detail. The only point of difference concerns the branch width, stated by Moore to be 0·25 mm, while in the Fermanagh material it ranges from 0·2–0·22 mm.

The Russian Upper Carboniferous species *M. ninae* (Viskova) 1961, corresponds so closely in all respects with the description of *M. plummerae*, and with the present specimens, that it is considered to be conspecific with them. The only discrepancies relate to the width of fenestrules and dissepiments (0·17–0·25 mm and 0·15–0·17 mm in the Russian form) and these are too small to warrant taxonomic attention.

M. praerhomboidea (Shulga-Nesterenko) 1951, is another Upper Carboniferous species probably conspecific with *M. plummerae*. It has a micrometric formula indistinguishable from that of the American species, though the branches and dissepiments are notably wider (0·3–0·4 mm and 0·15–0·25 mm respectively), and fenestrules correspondingly shorter and narrower. Such differences could be accounted for by the presence of thick secondary deposits on Shulga-Nesterenko's specimen, and her illustration (pl. XX, fig. 1) supports the idea. Despite the difference in branch width the zooecial base shape and size are the same as those of the present specimens.

M. rhomboidea (Nikiforova) 1938, has a slightly coarser meshwork than the Fermanagh material and the zooecial base shape is triangular rather than hemi-hexagonal. These features serve to differentiate this form, in which zooecial apertures and carinal nodes are also more widely spaced.

As Moore (1929 : 20) indicated, there is a similarity between *M. plummerae* and *F. mimica*, Ulrich, but this does not stand up to examination. The second species has a distinctly finer mesh with more apertures (24 per 5 mm), and the carinal nodes are in a single row.

Minilya binodata (Condra)

(Pl. 19, figs 5–7; Pl. 20, fig. 1)

1902 *Fenestella binodata* Condra; 350.
1903 *Fenestella binodata* Condra, Condra; 66, 110.
1957 *Fenestella binodata* Condra, Elias and Condra; 90.

Diagnosis. Compact colonial meshwork. Branch obverse gently convex: keel poorly developed; nodes small, obscure. Commonly an aperture at the end of each dissepiment and two along the intervening fenestrule margin.

Material. This is a rare form, of which only twelve small fragments were available. Several were partly replaced by beekite, and their finer structure obscured. The largest specimen measured 9 × 12 mm. PD.4828–31, PD.5256–8.

Measurements (N = 7):

	A	B	C	D
F.l.	0·82–0·87	0·853	0·023	2·66
F.w.	0·57–0·65	0·622	0·023	3·78
I.ap.s.	0·26–0·27	0·271	0·004	1·56
I.n.s. (in 1 row)	0·26–0·27	0·270	0·008	2·96
B.w.	0·27–0·30	0·296	0·007	2·53
Ap.d.	0·07–0·10	0·078	0·009	11·78
Diss.w.	0·12–0·17	0·153	0·017	10·75

Micrometric formula (based on seven specimens only): 15–16/11–13//18–20/18–19 (in 1 row).

In the specimens examined there are mostly three, but in some cases two, zooecial apertures per fenestrule.

Description. The available fragments indicate that complete zoaria were symmetrical, fan-shaped expansions. It is likely that colonies were of small size, probably 2–4 cm across. The meshwork is strong and compact, consisting of stout branches connected by short, thin dissepiments.

The obverse side of branches is rather flat, with a gently arched median crest but no pronounced keel. The reverse is rounded and faintly striated. There may be thick localized deposits of secondary schlerenchyma on this side, particularly where branches divide. The transverse section of branches is oval, with the long axis in the plane of the meshwork. At points of bifurcation branches may attain a width of up to 0·57 mm, decreasing immediately afterwards to about 0·25 mm.

The relatively short dissepiments are about half as wide as branches, and roughly circular in cross section. They increase considerably in width at either end, towards the union with branches. Spacing of dissepiments is regular, and they are almost level with the branch surface on the obverse, though somewhat depressed on the under side.

Fenestrules are basically rectangular with a length to width ratio of about two to one. They are mostly about one-and-a-half times as wide as branches. Superimposed on the rectangular shape, and to some extent obscuring it, are rounded extremities (due to the rapid increase in width at either end of dissepiments) and two rounded protrusions from the branch margin on each side. The last are most evident on the obverse surface.

Zooecial apertures are circular, close to the branch margin, and spaced about one-and-a-half diameters apart. They are regularly arranged, one opposite the end of each dissepiment and two along the side of the intervening fenestrule. In the latter situation the branch wall below an aperture commonly bulges into the fenestrule, causing the aperture itself to project in the same direction. Peristomes were not observed, but the outer apertural rim may be developed into a hood-like structure that emphasizes the beaded pattern of the branch margin.

The zooecial base shape could not be determined with certainty but it is most likely to be either a parallelogram or elongate-oval. The maximum length of each chamber is 0·17 mm, and the width perpendicular to this, 0·09 mm.

Carinal nodes are insignificant and difficult to identify, minute node-bases commonly providing the only indication of their former presence. Their disposition is in many cases obscure, though basically they are in two alternating rows, with a node corresponding to each zooecial aperture. The arrangement is locally confused and irregular, however, with the biserial pattern deteriorating for short distances into something approaching a ragged single line.

Ovicells similar in structure to those of *Fenestella* cf. *delicatula* (see Tavener-Smith, 1966a : 165) are present in some specimens. Each is found on the inner side (i.e. closer to the branch crest) of an associated zooecial tube and has the form of a deep, bowl-shaped concavity about 0·12 mm in diameter. The gonozooecial tube enters the brood chamber from below and to one side. The roof of the latter is invariably missing: no doubt it was of delicate construction and easily destroyed. One specimen showed quite a large number of ovicells grouped together. They are not restricted in occurrence to branch-dissepiment junctions, but generally distributed along the obverse of branches.

Discussion. The specimens appear to correspond closely with Condra's (1902) description of *Fenestella binodata* from the Coal Measures of Nebraska (Pennsylvanian), and are considered conspecific with that species. Owing to the presence of biserial carinal nodes, however, the form must be transferred to *Minilya*. Elias & Condra (1957 : 90) stated that the holotype has elongate-oval zooecial base shapes, and it is possible that in the Fermanagh specimens this is also the case. In describing *F. binodata* var. *wolfcampensis*, a Lower Permian variety hardly distinguishable from the parent species, Elias & Condra estimated the size of complete colonies to be 'about 20–25 mm high and 30–40 mm wide', figures very similar to those suggested above.

The specimens bear a general resemblance to *M. nodulosa* (Phillips), also found in the Carrick Lough residues (Tavener-Smith 1965a). That form has two and not three apertures per fenestrule, and its zooecial apertures and nodes are notably more widely spaced. It also has shorter but wider fenestrules and much wider branches.

Fenestella triserialis Ulrich 1890 is in many respects similar to the specimens described here, and its dimensions are also closely comparable. That species has triangular zooecial base shapes, however, and Ulrich's illustration (pl. L, fig. 4) clearly shows that the carinal nodes are uniserial.

Fenestella colymaensis Nekhoroshev 1935 and *F. benskiensis* Shulga-Nesterenko 1951, are other species structurally similar to the present form. In both, however, carinal nodes are uniserial, and Shulga-Nesterenko's form has keeled dissepiments, a feature not shown by the Fermanagh specimens.

Minilya oculata (M'Coy)

(Pl. 20, figs 2–8)

1844 *Fenestella oculata* M'Coy; 203.
1961 *Fenestella oculata* M'Coy; Miller, 229.

Diagnosis. Branches wide in relation to compact meshwork; somewhat flattened, with low, rounded median crests. Fenestrules with broadly rounded extremities. Apertures large, prominent.

Material. This distinctive species is common in the Carrick Lough residues and more than a hundred and twenty fragments, representing all parts of colonies, were examined. The largest measured 23 × 14 mm. PD.4832–9, PD.5259–75.

Measurements (N = 25):

	A	B	C	D
F.l.	1·10–1·35	1·222	0·084	6·87
F.w.	0·65–0·90	0·780	0·066	8·46
I.ap.s.	0·30–0·35	0·315	0·011	3·64
I.n.s. (in 1 row)	0·30–0·35	0·328	0·016	4·88
B.w.	0·35–0·40	0·367	0·014	3·81
Ap.d.	0·10–0·12	0·111	0·011	9·73
Diss.w.	0·15–0·25	0·196	0·027	13·77

Micrometric formula: 12–16/8–10//15–17/14–16 (in 1 row).

Apertures per fenestrule.

Range of specimen modes:	3	4
Distribution of specimen modes:	21	4

Description. Complete zoaria were probably fan-shaped expansions a few centimetres across, and the growth posture (as indicated by a fragment attached to a *Rhabdomeson* colony) was at least partially erect. The meshwork is strong, compact and of medium texture.

Branches are stout in relation to meshwork texture, and commonly of about the same width as fenestrules. On the obverse there is a well-formed median ridge with a rounded crest; the reverse is broadly convex and without prominent striations. Where present, the latter are faint and widely spaced. In the proximal region the under side of branches may be thickly coated with secondary skeletal substance. At bifurcations the pattern is normally that of a tuning fork, new branches at first diverging at angles of 50–70°, then curving back almost at once into parallelism.

Although in the proximal parts of colonies branch division is mostly regular and symmetrical, departures from this pattern are fairly common. In some fragments a strong and persistent central branch fails to bifurcate for some distance, instead giving rise to a series of lateral branches that diverge at an angle on either side. Such an arrangement is reminiscent of *Ptylopora*. In other cases a thick central branch bifurcates near the growth origin, the two offshoots then continuing in parallelism for some distance without further bifurcation. However, each produces a series of lateral branches on its *outer* side, and these bifurcate to complete the flabelliform shape of the colony. This pattern presents obvious similarities to that of *Ptiloporella*. The width of the major branches in these cases commonly exceeds that of normal ones, and may attain 0·45 mm. An exceptional figure of 0·7 mm was recorded in a heavily encrusted specimen.

In many zoarial fragments creeping stolons of the ctenostome *Condranema* follow the obverse branch crests and ramify from them. In some cases the slender, silicified stolonic tubes rest on the surface, but in others they are partly immersed, forming deep grooved channels in the substance of branches.

Dissepiments are short and moderately depressed below branch level on both sides. They are commonly slender but, due to secondary encrustation, there is considerable variation in width ranging from about one-third that of branches to near equality with them. From the mid-part of a dissepiment the width increases considerably towards the union with adjacent branches.

Fenestrules are mostly elongate-oval, or rectangular with well-rounded extremities. In the proximal region, where the branch pattern is less stabilized than elsewhere, fenestrules may be elliptical. The long sides are straight or slightly indented by zooecial apertures.

Circular zooecial apertures are commonly large and prominent. Peristomes are mostly lacking (possibly due to post-mortem abrasion) but where present they are plain, collar-like rims, most evident on the outer side where they may protrude slightly into fenestrules. There is no constant spatial relationship between zooecial apertures and dissepiments. Zooecial chamber bases have an elongate, hemi-hexagonal shape. The short lateral walls are inclined towards the growth origin. Maximum length of the chamber is 0·4 mm, and the maximum width, 0·2 mm.

Carinal nodes are insignificant, pimple-like structures that in many fragments are poorly preserved and difficult to identify. The only indication of their former presence may be tiny circular or oval basal scars. There is approximately one node per zooecial aperture, and the spacing between nodes in the same row is unusually regular. Although nodes are basically in a double row along the median keel, the strict biserial pattern is not uniformly maintained. Locally the arrangement may be somewhat irregular and even raggedly uniserial. A clear transition from biserial to uniserial was not observed, however.

Some specimens also bear a row of small nodes along the reverse mid-line of branches. The arrangement is uniserial and the structures (each with a diameter of about 0·02 mm) are spaced approximately 0·12 mm apart.

Supporting spines are present on the obverse or reverse of some specimens, but are small in size and number. Lateral spines growing as branch continuations are common, however, and one of these attained a length of 4 mm. Its width decreased in that distance from 0·55 mm (branch width at the last aperture) to 0·37 mm.

Discussion. This form is M'Coy's (1844 : 203) *F. oculata*, which was redescribed by Miller (1961 : 229) on the basis of two of M'Coy's examples. Both are very small and unsuitable as type specimens, being tectonically deformed and (in the case of one of them) heavily re-crystallized. In neither specimen is the keel well preserved, and the biserial nature of the carinal nodes is, therefore, not evident. The presence of this feature, here recognized for the first time, requires the transfer of the species to *Minilya*. In other respects the material described responds well to Miller's description, though the fenestrules are slightly larger. This is probably because both M'Coy's specimens are heavily encrusted with secondary schlerenchyma.

It is fortunate that the Carrick Lough fragments are recognizably conspecific with M'Coy's form, for they are in a much better state of preservation than his material. In addition, by representing all parts of zoaria they provide a better understanding of the specific characteristics. Some specimens in the sample seem at first sight to differ from the holotype, but closer examination shows that they share all its essentials, and are united with it by intermediate forms.

Genus ***PTILOPORELLA*** Hall, 1885

Diagnosis. Like *Fenestella*, but with branches of two sizes. A few larger or primary ones give rise to smaller or secondary branches on one or both sides. As the frond expands further primaries may arise by bifurcation or lateral growth from earlier ones, and in this way a fan-shaped colony is formed.

Type species. *Fenestella* (*Ptiloporella*) *laticrescens* Hall 1887. Devonian, Ontario.

Ptiloporella varicosa (M'Coy)

(Pl. 21, figs 1–9)

1844 *Fenestella varicosa* M'Coy; 204.
1961 *'Fenestella' varicosa* M'Coy; Miller; 238.

DIAGNOSIS. *Ptiloporella* with distinctive flabellate meshwork of strong branches united by slender dissepiments. Branches have triangular cross section and high median keel. Apertures large; chambers trapezoidal.

MATERIAL. The strong meshwork and distinctive branch pattern of this common species differentiate it at once from other fenestrate forms in the Carrick Lough residues. More than eighty fragments were examined, of which the largest measured 35 × 20 mm. PD.4840–7, PD.5276–97.

Measurements (N = 30):

	A	B	C	D
F.l.	1·20–2·00	1·513	0·159	10·51
F.w.	0·75–1·00	0·908	0·790	8·70
I.ap.s.	0·35–0·40	0·366	0·016	4·31
I.n.s.	0·45–0·75	0·588	0·064	10·96
B.w. (Primary)	0·37–0·60	0·477	0·053	11·17
B.w. (Secondary)	0·25–0·35	0·287	0·025	8·80
Ap.d.	0·12–0·19	0·136	0·015	11·19
Diss.w.	0·11–0·22	0·158	0·026	16·77

Micrometric formula: 11–17/6–9//13–15/7–12.

Apertures per fenestrule.

Range of specimen modes:	2	3	4
Distribution of specimen modes:	4	23	3

DESCRIPTION. The fragmentary specimens examined indicate that zoaria in this species were slightly undulose, approximately fan-shaped expansions. Mature colonies were of fairly large size, probably 5–10 cm across.

The chief distinguishing features of these specimens are:

1. the peculiar branch pattern intermediate between those of *Fenestella* and *Ptylopora*, and
2. the presence of branches of two sizes in the meshwork.

Measurement shows that differentiation into primary and secondary branches is not clear cut, however, and that all gradations exist, from the thickest to the thinnest. Nevertheless, consideration of a large number of branches indicates that the mean widths of the two groups are quite distinct. Most primaries diverge from the growth origin towards the margins of the frond. While their vigour lasts they maintain their dimensions and direction, giving rise to numbers of secondary branches on either side. Distally, however, they tend to become thinner and bifurcate in the manner of *Fenestella*, eventually losing their distinctive appearance. Lateral, or secondary branches, are initially thin and many remain so throughout their length.

In some cases, however, there is a progressive increase in width until the branch attains the dimensions of a primary. It may then bud off a series of laterals before returning to its original condition, or terminating.

On the obverse of branches there is a well-developed keel-ridge bearing a single row of carinal nodes. On either side of the keel the branch surface slopes steeply away towards the fenestrules. The reverse is broadly rounded, and on this side the difference between primary and secondary branches is particularly evident. A thick coating of secondary tissue commonly obscures longitudinal striae, and these are never strongly developed. Sparsely distributed 'pores' on or near the reverse mid-line proved to be the base scars of small acuminate spines similar to those present on some species of *Fenestella*. They are elliptical, with a length of about 0·05 mm.

Dissepiments are thinner than branches and many are slender and bar-like. There is an increase in width at each end, as the junction with a branch is approached. The spacing of dissepiments is somewhat irregular and they are depressed below branch level on both surfaces. The cross-section is roughly circular and in the older parts of zoaria connecting bars are much thickened by secondary deposits.

Fenestrules show much variation in shape and size between specimens, and even within a single fragment. The unusually distinctive characteristics of this group make it evident that all the fragments are conspecific, and the diverse fenestrule sizes and shapes provide an important indication of the range of morphological variation that is possible within a species. The commonest shape is rectangular with rounded extremities, the length to width ratio varying from two to one (about 1·8 × 0·9 mm) to near equality. In the proximal region, where branches and dissepiments are secondarily thickened, fenestrules may be elliptical and differing shapes and sizes are commonly associated, giving the meshwork an irregular appearance. The long sides of fenestrules are mostly straight but may be slightly indented by projecting apertures.

Large and prominent zooecial apertures have circular or oval shapes and are relatively closely spaced. Although the spacing is regular the number of apertures per fenestrule is rather variable, due to the irregular disposition of dissepiments. Plain, low peristomes are evident in a few specimens but are rarely prominent, though they may cause a slight lateral projection into the fenestrule. Some fragments from the proximal region show apertures occupying shallow grooves on either side of the keel. This is due to heavy secondary accretion on the latter structure and also on the branch sides.

Zooecial chambers are regularly trapezoid in plan, and ten that were measured yielded the following average dimensions: length of longer side, 0·3 mm; length of shorter side, 0·1 mm; perpendicular width between these, 0·225 mm. Branch divisions appear to have been preceded by the appearance of a larger, polygonal chamber which budded twice. Simultaneous budding seems to have led to symmetrical branch division, or bifurcation, but otherwise the earlier (more vigorous) bud maintained the original axis of growth, while the other was off-set and gave rise to a lateral or secondary branch. In a few cases 'secondary' buds were displaced abnormally and directed out of the meshwork plane altogether. These produced aberrant branches that are really misdirected laterals. They are thin, weak-looking and grew from the meshwork at varying angles. For these reasons they could be mistaken for young adventitious colonies of another species. Careful examination reveals the above relationship, however, and it is evident that such branches are essentially similar to the rest of the colony.

Supporting spines up to 5 mm long occur on the obverse or reverse surface but are relatively uncommon. Lateral spines representing the continuation of normal branches are more numerous and attain lengths up to 3 mm. In these there is a marked decrease in branch height (from about 0·65 mm to about 0·42 mm) immediately after the last aperture. It is as if the zooidal line had for some reason aborted, leaving the outer schlerenchyma to continue and form a sterile spine.

Discussion. This form is M'Coy's *Fenestella varicosa*, and the data given above may be used to amplify and modernize his description. Owing to the distinctive branch pattern the species must, however, be transferred to *Ptiloporella* Hall. The branch pattern in question, being intermediate in character between those of *Fenestella* and *Ptylopora*, suggests that the three genera were successively evolved. The record of their stratigraphic appearance is entirely in accord with this possibility.

Genus ***HEMITRYPA*** Phillips, 1841

Diagnosis. Like *Fenestella*, but with a superstructure supported on carinal nodes, and consisting of a planar, honeycomb-textured lattice. One of the hexagonal openings of the lattice lies above each zooecial aperture, and there are, therefore, two rows of hexagons per branch.

Type species. *Hemitrypa oculata*, Phillips, 1841. Devonian, England.

Hemitrypa hibernica M'Coy

(Pl. 22, figs 1–10)

1844 *Hemitrypa hibernica* M'Coy; 205.
1893 *Hemitrypa hibernica* M'Coy; Cole; 138.
1960 ? *Hemitrypa reticulata* Burckle; 1091.
1927 cf. *Hemitrypa burulica* Nikiforova; 182.
1962b *Hemitrypa hibernica* M'Coy; Miller; 314.

Diagnosis. Fine-textured, cup-shaped colonial meshwork of strong, parallel branches and short, stout dissepiments. Fenestrules oval. High keel on branches with regularly spaced spines. Apertures large; closely spaced.

Material. This is the commonest fenestrate species in the etched residues and hundreds of fragments from all parts of colonies were examined. The largest was 83 × 42 mm in size. PD.4848–57, PD.5298–311, PD.5342, PD.5313–317.

Measurements (N = 30):

	A	B	C	D
F.l.	0·52–0·77	0·689	0·060	8·74
F.w.	0·45–0·62	0·537	0·046	8·48
I.ap.s.	0·22–0·27	0·249	0·011	4·61
I.n.s.	0·35–0·45	0·421	0·028	6·71
B.w.	0·25–0·32	0·287	0·018	6·26
Ap.d.	0·10–0·14	0·121	0·009	7·66
Diss.w.	0·11–0·25	0·179	0·044	24·41
Sup.l.	0·22–0·26	0·250	0·010	4·13
Sup.w.	0·27–0·32	0·285	0·017	6·19

Note: The dimension 'Superstructure length' refers to the length of one of the hexagons of the superstructure parallel to the branch axis. Measurement was made between the centres of bars at opposite ends of the hexagon. 'Superstructure width' was measured perpendicular to the above, also between the centres of an opposing pair of bars.

Micrometric formula: 18–22/13–18//18–21/11–13.

Apertures per fenestrule.

Range of specimen modes:	2	3
Distribution of specimen modes:	19	11

Description. The presence of a regular and symmetrical superstructure distinguishes this, the only species of *Hemitrypa*, from other fenestrate forms. Even without the superstructure, the regular branch system, evenly distributed apertures, numerous carinal nodes and commonly occurring ovicellular depressions (Tavener-Smith, 1966a: 195) render identification easy.

Many of the larger specimens belonged to a single, more or less complete colony that emerged from the matrix as etching proceeded. It had an upright growth position and consisted of a convoluted, foliaceous meshwork rising at least 70 mm from a cup-shaped growth origin. The diameter was about 60 mm at the rim, and the superstructure external. The general appearance was similar to that of modern fenestrate cheilostomes such as *Iodictyum.*

Branches are mostly straight, stout and bifurcate rarely except in the proximal region. They are unusually high (average of twelve branch heights: 0·45 mm) and for this reason the cross-section is commonly oval. On the obverse there is a prominent median keel with a row of strong and regularly spaced carinal nodes, which act as supports for the superstructure. The reverse is well-rounded and may bear fine striae, though these are commonly obscured by thick secondary deposits. Prior to branch division the width increases progressively over a distance of 4–8 mm to a maximum of about 0·62 mm at the point of bifurcation. Immediately beyond this each new branch is only about 0·25 mm wide.

Dissepiments are short and vary greatly in width; some are slender and rod-like, but the majority are stout. There is always a considerable widening from the mid-point towards the union with a branch. Dissepiments are depressed below branch level on both sides and, because in most cases the height (average of fifteen: 0·25 mm) exceeds the width, they have an oval cross-section.

Fenestrules are commonly narrower than branches. They are mostly elongate-oval, with a length to width ratio of between two and one-and-a-half to one. Zooecial apertures do not, as a rule, protrude into fenestrules, which have straight margins.

Apertures are large, circular and spaced about one diameter apart. Peristomes commonly occur as low rims, and are in some cases more strongly developed to form collar-like structures. These may project slightly beyond the branch margin, but this is rare. Although the spacing of apertures is regular, their occurrence is not stabilized with reference to that of dissepiments.

Zooecial base-shapes are hemi-hexagonal, the average measurements of fifteen being: maximum length, 0·262 mm; maximum width, 0·15 mm. The short proximal and distal walls of chambers are steeply inclined towards the growth origin.

Carinal nodes, in this genus more properly regarded as pillars supporting the superstructure, are uniserial and spaced regularly along the keel. Their height, from keel to superstructure, is approximately 0·25 mm and the cross-section is circular or oval. Where the superstructure is destroyed the nodes commonly present a strongly serrated appearance in profile. The superstructure itself is a thin, planar, lattice-like expanse of hexagon units associated into a honeycomb meshwork of uniform texture. Two rows of hexagons correspond to a branch, and each one is situated directly above a zooecial aperture. The junction between the hexagon rows above a branch is of stouter construction than that above adjacent fenestrules, and provides attachment points for the ends of the supporting carinal nodes (Miller, 1962b: text-fig. 1).

The bars of the superstructure carry axial canals radiating from the distal ends of carinal nodes. In the unsilicified state these canals were occupied by the primary calcareous skeleton, which has not been preserved.

Nodes are also commonly present on the under sides of branches. They may be low, conical structures up to 0·07 mm high and of about the same diameter. Such nodes are sparsely distributed (roughly 0·5 mm apart) near or on the reverse mid-line, commonly occurring opposite branch-dissepiment junctions. On other specimens nodes are of slightly smaller size, but more closely (though less regularly) spaced, the distance between them being 0·7–0·17 mm.

The presence of thick secondary deposits on the reverse side is a characteristic of this species, and dissepiments may be particularly affected causing them to project below branch level. When a number of dissepiments enlarged in this way are roughly in alignment, the thickening spreads across intervening branches to form a continuous rib-like encrustation. One or more such ribs may be present on the under side of a meshwork, particularly in the proximal region. They are roughly concentric with the growth origin, and must have helped to support the large fronds by stiffening them. The local increase of branch height in these cases may be great—from a norm of, say, 0·3 mm up to about 0·75 mm, almost all of the thickening being on the reverse side. Similar massive dissepimental arcs have been described by Koenig (1958) in *Fenestella albida*, *F. alternata* and *F. regalis*.

Supporting spines are present on the obverse and reverse of the meshwork and, less commonly, as lateral branch continuations. They may be up to 7 mm long, with basal diameters up to 0·62 mm. On the obverse spines rise from the superstructure and, at their bases, strands of supporting tissue extend over the surface in many directions. It is notable that the main mass of a spine is derived from this level rather than from the branch. For example, a large spine with basal diameter 0·52 mm at superstructure level could be traced downward into two thickened (and distally amalgamated) carinal nodes whose aggregate diameter was only 0·2 mm. It is not clear which of them (if either) contained the axial material of the spine.

Discussion. This form is *Hemitrypa hibernica*, as the specimens correspond in all respects with M'Coy's (1844 : 205) description, and also with that of Miller (1962b : 314) who gave a revised account of the species. The present data, drawn from a larger sample, are of use in amplifying existing concepts of the species and providing an idea of the degree of variation within it.

The most distinctive feature of *Hemitrypa* is the honeycomb-patterned superstructure, and there is little doubt that this developed from the carinal nodes and had a protective function. Miller's (1962b : 318) suggestion that extended polypides actually protruded beyond the superstructure is unlikely to be correct, however. Measurement of the cross-sections of twelve meshworks yielded the following mean figures: height of branch, 0·33 mm; height of zooecial chamber, 0·175 mm; height of centre of superstructure above keel, 0·275 mm. It is, therefore, probable that the extruded polypides functioned between branch surface and superstructure, the latter affording a protective screen.

The thickened dissepimental arcs on the reverse of meshworks were most likely formed during pauses in the forward growth of a colony. They therefore represent stages in the colonial development and are crude 'growth lines'. During intervals of this kind zooecial budding appears to have been inhibited and no primary skeleton laid down. Secondary deposition did not cease, however, but continued along a front that remained static, and the massive, arcuate ribs resulted.

Genus ***POLYPORA*** M'Coy, 1844

Emended diagnosis. Planar, funnel or cup-shaped fenestrate expansions of radiating, straight or gently sinuous branches connected by regularly disposed, transverse dissepiments. Branches bear three or more rows of zooecial apertures on one side only; dissepiments are sterile. Obverse of branch smooth or with low longitudinal ridges separating rows of apertures. Ridges may bear low nodes. Reverse smooth, or longitudinally striate, with or without nodes.

Type species. *P. dendroides* M'Coy 1844. Tournaisian, Ireland.

Polypora dendroides M'Coy

(Pl. 23, figs 1–7)

1844 *Polypora dendroides* M'Coy; 206.
1963 *Polypora dendroides* M'Coy; Miller; 167.

Diagnosis. Robust meshwork of strong, roughly cylindroid branches, joined by short, stout dissepiments. Fenestrules oval to elliptical. Branch obverse somewhat flattened, with three to six rows of apertures and sparsely distributed small nodes.

Material. This is an uncommon form in the residues and only eight fragments were available. Six were well enough preserved to provide measurements. Due to the small number of specimens, and to the fact that all may have belonged to a single colony, the statistics given below do not provide an entirely adequate basis for comparison. The largest fragment was 17 × 15 mm in size. PD.4865–9, PD.5318.

Measurements (N = 6):

	A	B	C	D
F.l.	2·00–2·80	2·367	0·260	10·98
F.w.	1·30–1·60	1·467	0·090	6·13
I.ap.s. (in 1 row)	0·37–0·40	0·392	0·009	2·36
I.ap.s. (diagonally)	0·30–0·32	0·312	0·012	4·00
B.w.	0·75–1·07	0·088	0·013	15·01
Diss.w.	0·45–0·75	0·579	0·092	15·92

Micrometric formula (based on six fragments): 6–8/4–5//12–13.

Apertures per fenestrule.

Range of specimen modes:	3	4	5
Distribution of specimen modes:	1	3	2

Number of rows of apertures per branch: three to six, usually four.

Description. The available fragments do not indicate with certainty the original zoarial shape, but it is likely that this was a flat fan-shaped expansion. In several specimens branches divide repeatedly and are thickly coated with secondary material, particularly on the reverse. These appear to have belonged to the proximal region. Branches are in general very stout in comparison with fenestrule width and have a roughly circular cross-section. The obverse is somewhat flattened, notably in the wider part that precedes branch division, and the under side may show numerous, fine, closely spaced longitudinal striae. In some specimens the meshwork is irregular and branches seem to have obstructed one another during growth.

Dissepiments are short and stout (being commonly much thickened by secondary schlerenchyma), and not always uniformly spaced. They have a circular transverse section and are slightly depressed below branch level on the obverse, though more so on the under side. The width of the central part of dissepiments is mostly about half that of branches, though it increases greatly at either end.

Fenestrules vary considerably in size, particularly in length. They are mostly oval or elliptical, and have straight sides uninterrupted by projecting apertures.

Zooecial apertures are in four or five rows on the obverse of branches. The number may increase to six at bifurcations, decreasing to three immediately thereafter. The division into rows is not always clear and locally the arrangement may be somewhat confused. Apertures are circular or oval, but measurement is commonly hampered by thick secondary deposits that partly or wholly obscure the openings. Circular apertures are about 0·12 mm in diameter while in oval ones the major axis has a length of about 0·22 mm.

Zooecial chamber bases are rhombic or lozenge-shaped in the internal rows, while those along branch margins are hemi-hexagonal or irregularly five-sided. Chamber walls are not quite perpendicular to the base, but inclined steeply towards the growth origin.

Carinal nodes do not occur in *Polypora*, there being no median keel, but sparsely distributed nodes may be present on the obverse, in some cases on low ridges that separate rows of apertures. In the present specimens a few small base-scars and truncated stumps mark the former position of nodes, but they do not appear to have had a regular arrangement.

Another feature of the obverse of several specimens is the presence of stout spines, from the proximal ends of which rope-like strands of supporting tissue ramify over the surfaces of adjacent branches and dissepiments. These anchoring strands are of striated secondary schlerenchyma, and pass distally into the outer investment of the colonial surface. In fragments from the proximal region, the amount of secondary encrustation associated with the spines is so great that fenestrules have been sealed and apertures occluded in considerable numbers. The purpose of the structures, which must have been of considerable size, is unknown but comparison with other fenestrate species suggests that they had a supporting role.

Shorter and less robust spines grow from the reverse surface of some specimens. These are all truncated at the distal ends, but may be up to 5 mm long.

Discussion. The material described here corresponds closely with the type specimens and descriptions (M'Coy 1844 : 206; Miller 1963 : 167) of *Polypora dendroides*, and is assigned to that species. The original specimens came from the Tournaisian of Hook Head, Co. Wexford. A thin section used by Miller in redescribing the form shows that chamber bases have the same shape as those described above.

Polypora verrucosa M'Coy

(Pl. 24, figs 1–7)

1844 *Polypora verrucosa* M'Coy; 206.
1963 *Polypora verrucosa* M'Coy; Miller; 169.

Diagnosis. Open-textured meshwork of strong branches and slender dissepiments; fenestrules rectangular. Branches flattened on obverse, with three to five rows of apertures. Peristomes may indent fenestrules. Zooecia tubular, with lozenge-shaped or triangular bases.

Material. This is the commonest *Polypora* and its fragments, present in abundance, constitute a distinctive element of the fauna. More than a hundred and fifty were examined, the largest measuring 28 × 16 mm. PD.4870–7, PD.5319–30.

Measurements (N = 20):

	A	B	C	D
F.l.	3·30–4·70	4·135	0·376	9·09
F.w.	1·40–2·20	1·755	0·183	10·43
I.ap.s. (in 1 row)	0·35–0·42	0·385	0·020	5·19
I.ap.s. (diagonally)	0·22–0·32	0·261	0·022	8·23
B.w.	0·52–0·70	0·630	0·044	7·06
Ap.d.	0·10–0·12	0·117	0·009	7·45
Diss.w.	0·25–0·35	0·287	0·031	10·78

Micrometric formula: 5–8/2–3//11–14.

Apertures per fenestrule.

Range of specimen modes:	8	9	10	11	12
Distribution of specimen modes:	5	6	4	4	1

Number of rows of apertures per branch: Three to five, usually four.

DESCRIPTION. This striking form cannot be confused with any other in the etched residues. The coarse textured and rigid-looking meshwork consists of straight, strong branches connected by relatively thin, bar-like dissepiments. Complete colonies were probably large, roughly planar expansions, but there is nothing to indicate whether the growth habit was erect or otherwise.

Branches are broad, flattened on the obverse, and decorated on that side by gently sinuous, longitudinal ridges and furrows sweeping round and between apertures and nodes. On the reverse both sides slope inward to form a blunt 'keel' that may be accentuated by selective secondary deposition. In cross-section, therefore, branches have the appearance of 'rounded triangles' with the apex downward. The under side is longitudinally striated, with about a dozen fine, closely-spaced ridges, the counterparts of those more prominently developed on the obverse. The striated nature may be obscured by secondary schlerenchyma, particularly on the reverse, where this can be so thick that silicious replacement has taken the form of concentric rings of beekite.

Dissepiments are relatively thin, bar-like and circular in cross-section. There is an increase in width at either end approaching the union with a branch, but it is not great. Spacing is fairly regular, and longitudinal ridges and furrows on the cross-bar curve into continuity with corresponding structures on adjacent branches. Dissepiments are strongly depressed on the obverse, but on the reverse are about level with branches, or even slightly bowed so that they project below them.

The large fenestrules are mostly elongate-rectangular but in some cases elongate-oval. On the reverse their lateral margins may be regularly indented by protruding apertures: this is less evident on the upper surface.

Circular zooecial apertures are in four longitudinal rows on each branch, the number increasing to five before bifurcations and decreasing to three immediately afterwards. Peristomes are variably developed and may be prominent. They appear initially as collar-like rims round apertures, but continued growth results in the formation of a rounded-conical tumidity with a terminal aperture. The latter is, of course, a secondary structure with slightly reduced diameter (average of six measured: 0·1 mm). The presence of strongly developed peristomes may give a coarsely nodular appearance to branches and, in the case of marginal rows, the structures may notably indent fenestrule margins.

Zooecial chambers are elongate tubes and not box-like. They are inclined at 25-45° to the lower surface of a branch and, therefore, have relatively small base areas. These are rhombic or lozenge-shaped in the inner rows, with a maximum length of about 0·27 mm, and maximum width about 0·15 mm. In rows bordering fenestrules the shape is triangular, with similar length but slightly reduced width (about 0·12 mm).

Small and insignificant nodes are present at irregular intervals (1·25–2·0 mm) along the obverse mid-line of branches. They are not on a ridge or keel, but rise directly from the branch surface between the inner rows of apertures.

Discussion. The specimens correspond in all respects to descriptions of *Polypora verrucosa* by M'Coy (1844 : 206) and Miller (1963 : 169), and undoubtedly belong to that species. M'Coy's type material came from the 'Carboniferous Upper Limestone' at Black Lion, Co. Cavan, a few miles from Carrick Lough and at approximately the same horizon. The holotype shows the streamlining of ridges and furrows round apertures more clearly than the Carrick Lough material, though the characteristic 'warty' appearance to which the specific name refers is equally well developed in the latter.

Because of the apparent absence of nodes from the obverse mid-line of branches, and the presence of strong longitudinal ridges and grooves on that side, Miller (1963 : 169) only assigned this form to *Polypora* provisionally. He thought these features might have indicated the presence of a separate genus bearing the same relationship to *Polypora* as *Levifenestella* bears to *Fenestella*. However, the present specimens do show an irregular median line of small nodes, and the strongly striated obverse is merely an unusually pronounced manifestation of a condition that, at least potentially, exists in all Fenestellidae. There is, therefore, no reason for the erection of a new genus, and the form is here regarded as typical of *Polypora*.

Miller's (1963 : 166) emended diagnosis of the genus stated that there should be 'regularly spaced, elevated nodes on the central line of the obverse' of branches. This is an innovation, as no such requirement is included in earlier diagnoses, for example, those of M'Coy 1844 : 206; Nickles & Bassler 1900 : 39; Bassler 1953 : G125; or the Russian Treatise 1960 : 80. The view of these authorities is adequately reflected by the statement of Nickles and Bassler that in the genus branches 'lack the median keel, though this is *sometimes* represented by a row of strong nodes or tubercles' (the writer's italics). It is implicit in this statement that not all species of *Polypora* possess such nodes, and their presence is not therefore diagnostic. The generally-held concept of the genus has not radically changed in recent years, and Miller's requirement in respect of nodes must be rejected as unwarranted and over-restrictive.

Family **ACANTHOCLADIIDAE** Zittel, 1880

DIAGNOSIS. Zoarium a pinnate or fenestrate expansion, celluliferous on one face only, consisting of strong central stems which give off numerous smaller lateral branches from their margins; the lateral branches are free, or unite with those of the next stem; non-poriferous dissepiments rarely present; zooecial characters mostly as in the Fenestellidae (Nickles and Bassler 1900: 41).

Genus ***PTYLOPORA*** M'Coy, 1844

DIAGNOSIS. Fan or funnel shaped, attached by roots from which a strong midrib arises, giving origin on each side to thin, equidistant branches, connected by regular dissepiments; external face of the branches carinate, and bearing two rows of zooecial apertures. (Based on M'Coy 1844: 200.)

TYPE SPECIES. *P. pluma* M'Coy 1844. Tournaisian, Hook Head, Ireland.

Ptylopora pluma M'Coy ***parva*** subsp. nov.

(Pl. 25, figs 1–10)

MATERIAL. Only a few small specimens were available, mostly with a well-developed primary branch but relatively little of the meshwork. One showed the proximal region with a well-preserved basal holdfast. The broken ends of strong primary branches commonly showed the interior in an excellent state of preservation and yielded valuable information about skeletal structure, which is identical to that of the Fenestellidae. The largest fragment measured 13 × 10 mm. PD.4883, PD.4878–82, PD.5331–5.

Measurements (N = 12):

	A	B	C	D
F.l.	0·85–1·05	0·954	0·072	7·57
F.w.	0·55–0·82	0·635	0·069	10·94
Primary measurements				
B.w.	0·47–0·80	0·612	0·092	15·10
I.ap.s.	0·30–0·35	0·321	0·014	4·36
I.n.s.	0·17–0·35	0·256	0·049	19·12
Ap.d.	0·09–0·11	0·104	0·004	2·06
Secondary measurements				
B.w.	0·27–0·37	0·310	0·031	9·82
I.ap.s.	0·25–0·30	0·283	0·020	6·97
I.n.s.	0·20–0·27	0·235	0·023	9·77
Ap.d.	0·09–0·11	0·097	0·010	10·34
Diss.w.	0·10–0·22	0·157	0·028	17·96

Note: 'Primary' measurements refer to the strong midrib, while the others apply to the laterally developed meshwork. Care must be exercised in using the width of the midrib for comparative purposes, for this tapers distally.

Micrometric formula of meshwork: 14–18/9–13//17–20/18–25.

Apertures per fenestrule.

Range of specimen modes:	2	3	4
Distribution of specimen modes:	1	10	1

Diagnosis. Small *Ptylopora* structurally similar to *P. pluma,* from which it differs in having shorter fenestrules, thinner secondary branches and more closely spaced carinal nodes. Dimensions are stated above.

Type specimens. Holotype: PD.4883. Paratypes: PD.4878 to PD.4882.

Description. The zoarial shape was penniform, with a midrib of considerable length (the longest specimen, which was incomplete, measured 28 mm) supporting a *Fenestella*-like meshwork on either side. The divergence angle of lateral branches varied from 44–68°, the average in twelve specimens being 60·5°. The presence of a specimen with a heavily calcified basal holdfast and supporting processes suggested that colonies grew in an upright, or partly upright position.

The primary branch is strong, straight and distally tapered. A prominent, rib-like median keel, rising abruptly from the somewhat flattened obverse surface, takes up about one-third of the branch width, and close to this on each side is a row of small zooecial apertures. These may lie in longitudinal grooves representing areas of minimum secondary accretion between zones of much greater thickening on either side. The broadly rounded reverse commonly bears about a dozen fine, closely-spaced longitudinal ridges, each with a row of minute papillae on its crest. These have a diameter of about 0·02 mm and are spaced about the same distance apart. The reverse of some specimens is smoothly rounded, however, and without ridges or striations, though there are numerous papillae streamed generally parallel with the branch length.

Ridges and striations are also present on the obverse, though they are hardly visible and have a less regular arrangement. Papillae are numerous but appear to be randomly distributed and do not form rows except along the keel. This commonly consists of three or four closely associated and clearly marked longitudinal ridges, one of which may be accentuated to form the crest. Along it a row of papillae may be visible between successive carinal node bases.

The holdfast is a thickened, stalk-like proximal part of the midrib from which lateral branches have been stripped or where, perhaps, they never existed. Its length, from proximal extremity to the first lateral branch, is 10 mm, and the maximum width, 1 mm. At its termination the heavily calcified stalk gives rise to a number of supporting or anchoring processes, between some of which there are slender connecting bars.

Secondary, lateral or side branches are more slender than the main one, which projects below them considerably. They diverge from it at intervals of 0·6–0·8 mm on either side, are more or less straight, and do not bifurcate. On the obverse the sides of branches slope steeply away from a median keel that resembles the ridge of a roof and in this respect differs from the prominent rib-like structure on the primary branch. At junctions with the latter it is evident that the two kinds of keel are not continuous, there being a flat, keel-less area between them. The reverse is rounded and commonly bears closely spaced longitudinal ridges with rows of papillae along their crests. At junctions the ridges and furrows of lateral branches merge with those on the midrib, and the rows of papillae do likewise.

Dissepiments are short and slender in most cases, though when coated with secondary schlerenchyma they may be relatively stout. There is a considerable increase in width at each end, close to the union with a branch. Dissepiments, which are approximately circular in cross-section, are clearly depressed below branch level on the obverse, but less obviously on the under side. They are axially striated, with rows of papillae along ridge crests, as with branches. Laterally adjacent dissepiments tend to be situated the same distance from the main branch, with their ends roughly in apposition, so that they form a more or less continuous dissepimental zone. There are a series of these zones on either side of the primary branch and roughly parallel with it.

Due to the terminal increase in dissepimental width, fenestrules are mostly elongate-oval, though they may be elliptical or rectangular. The long sides are straight and uninterrupted by projecting apertures.

Two rows of zooecial apertures are situated close to the keel and away from branch margins. They are circular or oval, in the second case measuring about 0·12 by 0·07 mm. The apertures are relatively small and spaced from one to two diameters

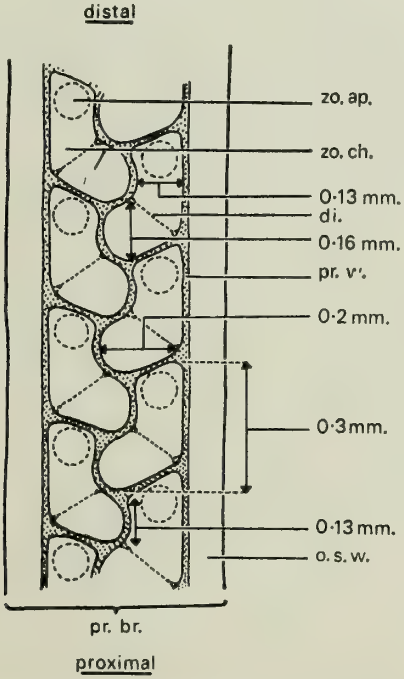

Fig. 5. Shape and dimensions of zooecial chambers in a primary branch of *Ptylopora pluma parva*. di., diaphragm; o.s.w., outer secondary wall; pr.br., primary branch; pr.w., primary wall; zo.ap., zooecial aperture; zo.ch., zooecial chamber.

apart; the diameter and spacing being slightly greater on primary branches than on secondary ones. There are no noticeable peristomes.

The zooecium has an unusual plan, consisting of a roughly D-shaped proximal chamber that continues into a broad tube directed at about 45° to the upright of the D. The tube is separated from the chamber by a well developed hemiseptum, and has the aperture at its distal end. Within a branch the relatively wide proximal part of a zooecium opposes the narrower distal part of the next, so that they fit closely together in alternating rows. The arrangement is shown, together with dimensions, in the accompanying diagram (fig. 4).

Small, though prominent carinal nodes are present on primary and secondary branches. On the former they are about 0·12 mm high, compared with a branch height of about 0·5 mm. The nodes of secondary branches are mostly missing, but their former positions are marked by small, oval, base-scars.

A few obliquely directed supporting spines with broken distal ends are present on the reverse of specimens. They are up to 5 mm long and 0·5 mm in diameter at the base. A single lateral spine, representing the sterile continuation of a secondary branch, extended for 1 mm beyond the last zooecial aperture and was 0·2 mm wide.

Discussion. The specimens are superficially similar to M'Coy's *P. pluma* from the Carboniferous Slate of Hook Head, Co. Wexford, but there are dimensional differences. The holotype has the formula: 13–16/7–8//15–18/10–14, and secondary branches diverge from the midrib at 50–55°. Fenestrules are longer than in the Fermanagh specimens (average length: 1·1 mm compared with 0·95 mm), secondary branches are wider (0·39 mm against 0·31 mm) and carinal nodes further apart (average internodal distance on meshwork: 0·425 mm compared with 0·235 mm). Dissepiments are also much stouter on M'Coy's specimen, and although age differences might explain this, they cannot satisfactorily account for the discrepancy in branch width. It is true that the Fermanagh sample is small and may consist of immature colonies, nevertheless, there are appreciable differences from the holotype and, as the material is from another horizon and locality, it seems advisable to refer it to a separate subspecies. The overall structural similarity with M'Coy's material prompts the writer to retain the specimens within *P. pluma* however, a decision that is strengthened by Dresser's (unpublished thesis, 1960) discovery of specimens with intermediate characteristics in the C_2S_1 of Malahide, Co. Dublin. Her material (also referred to *P. pluma*) had the formula: 15–17/8–10//15–18/20–25.

Comparison of data by *t*-tests showed that in the etched specimens there is a significant difference ($P < 0·05$) between the spacing of zooecial apertures on primary and secondary branches, that of the former being greater. The diameter of apertures on primary branches is also significantly larger than that of secondary ones. In view of the greater width of the central branch it seems probable, therefore, that its zooecial chambers are slightly larger than those of lateral branches. Similar statistical tests showed that there is no significant difference ($P > 0·05$) between the spacing of carinal nodes on the two kinds of branches.

Cross-sections of some heavily encrusted branches showed that although the reverse surface may be smoothly rounded and without striae, secondary laminae within the branch become progressively more corrugated towards the axial region. This tendency reaches its maximum at the contact with the strongly ribbed under side of the basal plate, a part of the primary skeleton. The ribbing seen in cross-sections is merely a reflection of the striated or longitudinally ridged condition in solid specimens, and it therefore seems that although the presence or absence of 'striae' on the reverse may be an indication of the age, or the state of weathering of a specimen, it is unlikely to be of taxonomic value.

Genus ***SEPTOPORA*** Prout, 1859

Diagnosis. Zoarium a fenestrate, flabellate or leaf-like expansion; primary branches numerous; increasing by bifurcation or interpolation; the lateral branches unite with those from the adjacent primary branches; apertures in two rows on primary and lateral branches; reverse usually with fine striae and scattered dimorphic pores (Nickles & Bassler 1900: 41).

Type species. *S. cestriensis* Prout 1859. Mississippian, Illinois.

Septopora hibernica sp. nov.

(Pl. 26, figs 1–8)

Material. Only ten specimens were available. They are not in such good condition as those of other species, being encrusted with secondary tissue to an unusual degree, so that surface features are commonly obscured. Some branches lack the entire apertural face, presumably owing to partial replacement, so that only the base and sides remain. It is possible that all specimens belonged to a single colony, and this should not be overlooked in using the following data for comparative purposes. The largest fragment was 42 × 17 mm. PD.4885–91, PD.5336–8.

Measurements (N = 10):

	A	B	C	D
F.l.	1·20–1·50	1·400	0·100	7·14
F.w.	1·50–2·00	1·640	0·156	9·51
I.ap.s.	0·35–0·40	0·375	0·011	3·00
B.w. (primary)	0·72–0·87	0·770	0·043	5·58
B.w. (secondary)	0·45–0·67	0·515	0·070	13·59

Note: Data for zooecial apertures are not included as these structures are commonly broken, abraded, or so reduced by coarse grained silicification that original dimensions are not evident.

Micrometric formula: 6–8/7–9//12–14/none.

Apertures per fenestrule.

Range of specimen modes:	3
Distribution of specimen modes:	10

Diagnosis. *Septopora* of unknown zoarial shape, lacking carinal nodes and 'dimorphic pores'. With well developed keel on primary, but not secondary branches. The latter have a variable growth habit, causing fenestrule shapes to be irregular. Primary branches may show a *Ptylopora*-like pattern and bear two rows of small, closely-spaced zooecial apertures. Chamber base shapes triangular or hemi-hexagonal with short lateral walls. Structural data as above.

TYPE SPECIMENS. Holotype: PD.4885. Paratypes: PD.4886 to PD.4890.

DESCRIPTION. There is no certain evidence of zoarial shape though, judging from the structure of available fragments, it was probably a more or less upright, foliaceous or fan-shaped growth. Two of the larger fragments have a pronounced *Ptylopora*-like branch pattern and are only distinguishable from that genus by the cross-bars (secondary branches) which bear zooecia.

Primary branches are straight or gently flexed. They are stout and somewhat flattened on the obverse, which bears a prominent, rib-like median keel. In shallow, longitudinal grooves on either side of this are two rows of zooecial apertures. The reverse is broadly rounded and longitudinally striated, the striae serving to separate a number of ridges, each of which bears on its crest a row of minute, rounded papillae. These are about 0·01 mm in diameter and spaced about 0·04 mm apart. From eight to ten parallel ridges are visible on the reverse of a branch.

Secondary branches (corresponding to dissepiments in the Fenestellidae) are variably developed, and their original shapes are commonly obscured by heavy secondary deposits. Where two unite in the chevron pattern characteristic of *Septopora*, they leave the main branches at angles of about 50°. This arrangement is uncommon in the present material in which, owing to space restriction and irregularities of growth, others predominate. Close to the junction of primary branches secondaries may be short and straight, rather like stout fenestellid dissepiments. In other cases a secondary appears to have developed independently of its partner, forming an oblique cross bar between adjacent primary branches. Bow-shapes are of fairly common occurrence, the angular junction between components having been rounded by later schlerenchymal growth. In other examples irregular shapes have resulted from asymmetrical unions between opposing secondary branches. Well developed secondaries have two rows of alternating apertures, but in many cases the arrangement is irregular. Some appear to lack apertures altogether, but this is probably due to sealing by schlerenchymal overgrowth rather than to a genuine absence of zooecia. Secondary branches do not have a median keel and the cross-section is approximately circular. The reverse shows the same characteristics as in primaries.

Fenestrules in *Septopora* are typically chevron-shaped with rounded extremities, but these are rare in the present specimens. The irregular growth of secondary branches inevitably results in many variations of fenestrule shape, which may be round, oval, rectangular or even triangular. Variable amounts of secondary encrustation cause still further diversity and commonly convert regular to irregular shapes. The relatively small size of fenestrules and their variable configuration might almost be said to characterize the specimens examined.

Zooecial apertures are in two alternating rows close to the keel and away from branch margins. They may be circular, with a diameter of about 0·15 mm, or (more commonly) oval, measuring about 0·225 by 0·125 mm. Some are relatively small and more than their own diameter apart; others are much larger and separated by only a thin bar. Much depends on the amount of secondary encrustation present, for there is no doubt that this has in many cases reduced the size of apertures or even sealed them altogether. On the other hand, many have been enlarged by breakage or incomplete replacement of their rims. Apertures on both kinds of branches were probably of about the same size.

Few zooecial base shapes are distinguishable in the specimens, but it is possible that there is a slight difference in this respect between primary and secondary branches. Those of the former seem to have hemi-hexagonal shapes with a length of about 0·32 mm and maximum width of 0·2 mm. The short lateral walls are about 0·05 mm long. On secondary branches chambers appear to be of similar size but triangular, with the maximum length (parallel to the branch margin) about 0·3 mm and maximum width about 0·25 mm. Only three chamber bases of each kind were seen, however, and it is uncertain whether the observed difference is general or not.

Discussion. This is the first positive record of *Septopora* in the British Isles, though Whidborne (1895, p. 183) mistakenly assigned a poorly preserved specimen (probably of *Ptiloporella*) to the genus. Nor has *Septopora* been found in other European countries, with the exception of Russia where a number of species have been reported in recent years (Nikiforova 1938; Shishova 1952, 1957; Morozova 1955). The genus was introduced by Prout in the United States, and several species were described by Ulrich (1890). A possible reason for the previous absence of *Septopora* from faunal lists is that, due to lines of weakness provided by the angular junctions between secondary branches, the colonies were particularly liable to breakage. The resultant fragments typically consist of a primary branch with a number of secondaries on each side, all broken at the junction angle. Such fragments are exceedingly difficult to distinguish from *Penniretepora* stipes (always abundant in Carboniferous bryozoan faunas) and could easily have been described as such in the literature.

Among described forms of *Septopora* the present specimens are closest to the type species, which is from approximately the same horizon (lower Chester) in Illinois. Common features include a clear median keel on the obverse, about three zooecial apertures per fenestrule and the absence of small accessory apertures ('dimorphic pores'). There are also important differences, however, *S. cestriensis* having a rather finer mesh (ten or eleven branches and fenestrules in 10 mm, according to Prout), carinal nodes and apertural peristomes. Ulrich (1890; 628) recorded the species from the lower and middle Chester of Illinois and Kentucky, but his specimens had an even finer meshwork than those of Prout. He also mentioned the presence of accessory pores on both obverse and reverse, a feature not shown by Prout's specimens or the present ones. The average branch width of Ulrich's material was 0·5 mm, considerably less than that of the Irish specimens, though this might be accounted for by the thick secondary encrustation of the latter. Shishova (1952; 162) found, in the Dinantian of the Moscow region, specimens that she assigned to *S. cestriensis*. She stated their formula as: 14/10½–11½//22–22½, which differs widely from that of the Fermanagh specimens. Also her material had lozenge-shaped (rhomboidal) chamber bases, and there were accessory pores on the reverse.

The only other described species which the present specimens resemble is *S. subquadrans* Ulrich, from the upper Chester. This differs from *S. cestriensis* mainly in fenestrule shape, and has the formula: 7–12/10½–12//21. The number of apertures per 5 mm is greatly in excess of that shown by the Fermanagh specimens, however, and there are accessory apertures on both surfaces (Ulrich 1890; 629).

In view of the lack of correspondence with existing species it is clearly necessary to introduce a new name for the present material. *S. hibernica* seems appropriate for the first recorded occurrence of the genus in Ireland.

Other Genera

Note: In addition to the above forms, three further fenestrate bryozoans belonging to the Carrick Lough fauna have been described separately elsewhere by the author. In each case the account given follows the basic pattern used here. The additional species and location of their descriptions are:

1. *Ptilofenestella carrickensis* gen. et sp. nov. In 1965, *Palaeontology* **8** : 478–491.
2. *Minilya nodulosa* (Phillips). In 1965, *Geol. Mag.* **102** : 135–142.
3. *Polypora stenostoma* sp. nov. In 1971, *Palaeontology* **14** : 178–187.

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PLATE 1

Fenestella frutex M'Coy

FIG. 1. Obverse of large zoarial fragment, with an encrusting stenoporid colony. PD.5001.* ×2·9.

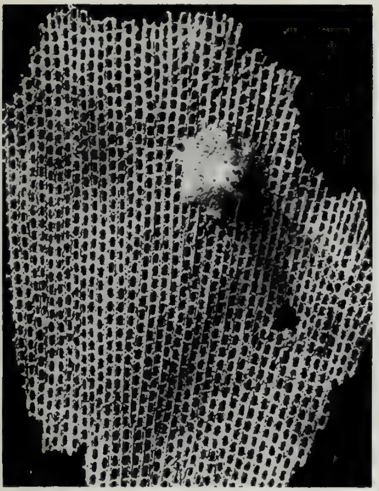
FIGS 2, 3, 5, 6. Obverse of small zoarial fragments to illustrate common variations in meshwork appearance. PD.5002 to PD.5005, ×6·0; ×5·0; ×6·7; ×5·6, respectively.

FIG. 4. Stout, barbed spines from the obverse surface to the meshwork. PD.5006. ×4·5.

FIGS 7, 9. Detail of the obverse surfaces of morphological variants within this species. PD.5005, ×18·0; and PD.5002, ×21·0.

FIG. 8. Reverse side of a zoarial fragment showing longitudinal 'striae' and minute nodes. PD.5007. ×5·8.

* The serial numbers of specimens refer to the Bryozoa catalogue numbers of the collections of the British Museum (Natural History), where the material is stored.



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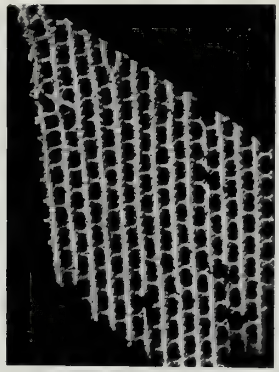

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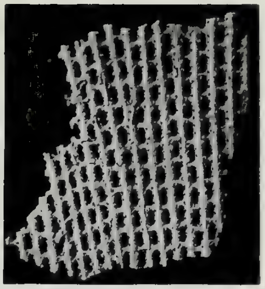

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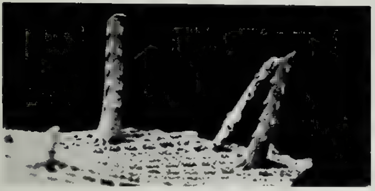

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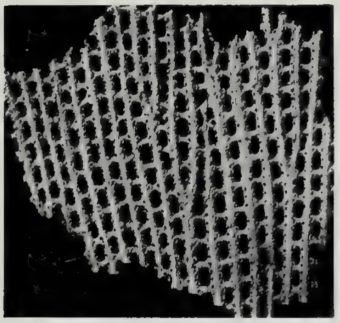

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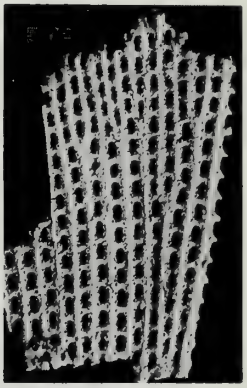

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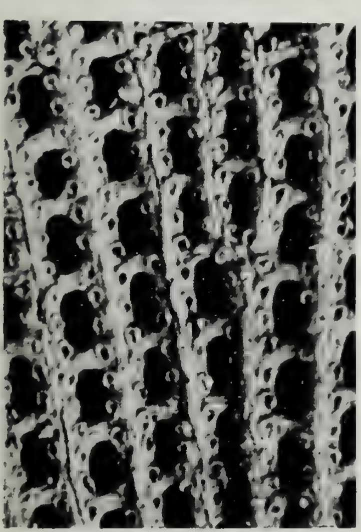

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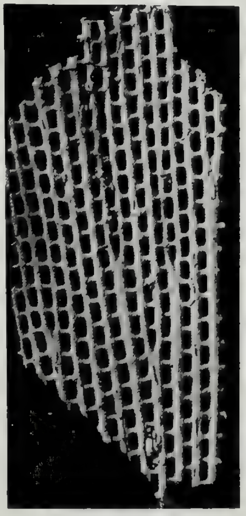

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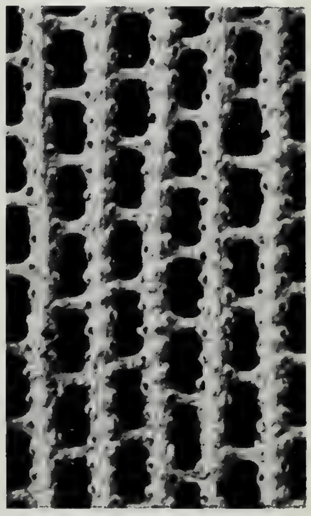

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PLATE 2

Fenestella ivanovi Shulga-Nesterenko

FIGS 1, 3, 5, 7. Obverse of zoarial fragments to show variations in meshwork pattern. PD.5008, ×6·0; and PD.4682 to PD.4684, ×5·0; ×5·3; ×5·0, respectively.

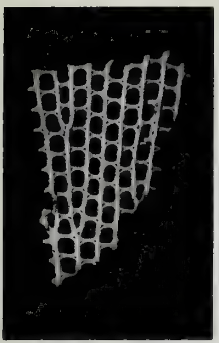
FIG. 2. Proximal part of a zoarium with basal holdfast and lateral supports; the last developed from marginal branches and dissepiments. PD.4685. ×5·2.

FIG. 4. Zoarial fragment with elongate spinose structures which are 'infertile' branch continuations. PD.4686. ×5·5.

FIG. 6. Delicate spines with minute barbs growing from the obverse sides of branches. PD.4687. ×5·0.

FIG. 8. Reverse surface of zoarial meshwork. PD.4684. ×17·0.

FIG. 9. Detail of obverse side showing the distinctive shape of fenestrules. PD.4685. ×16·0.



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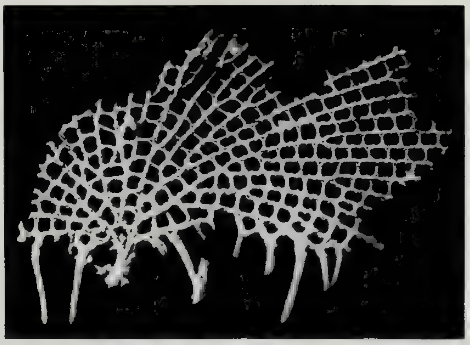

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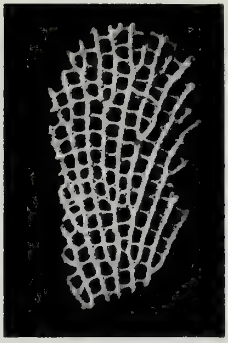

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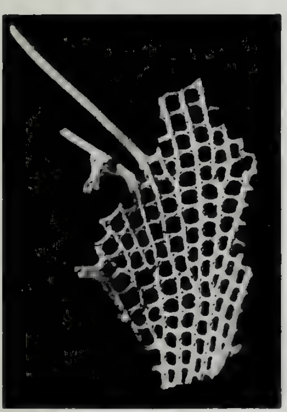

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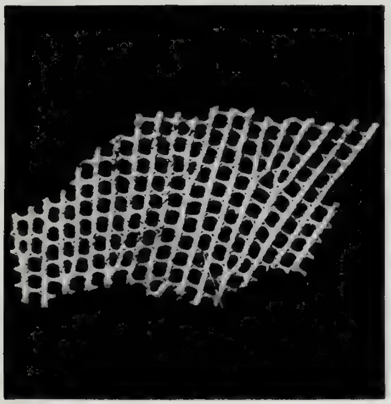

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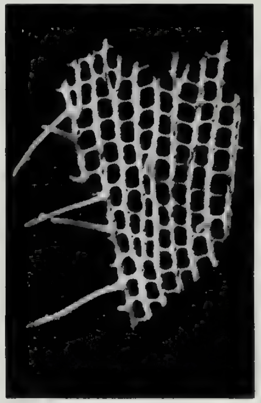

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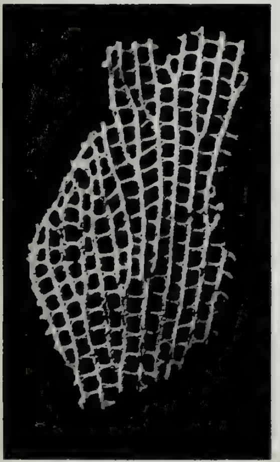

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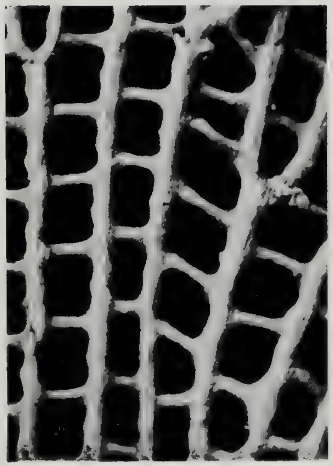

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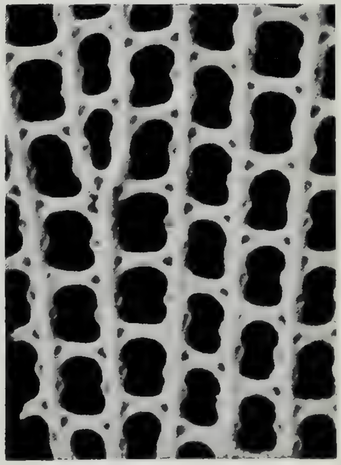

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PLATE 3

Fenestella cf. ***multispinosa*** Ulrich

FIG. 1. Reverse of zoarial meshwork showing longitudinal 'striae' and nodes on the mid-line of branches. PD.4688. ×5·7.

FIG. 2. Another view of the reverse surface. PD.4689. ×5·0.

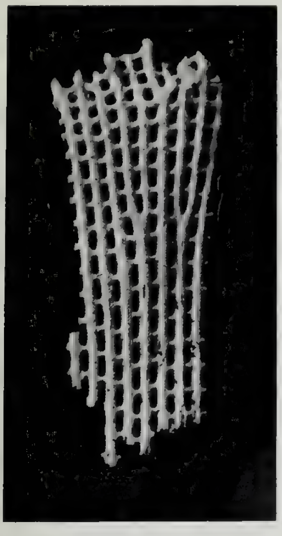
FIGS 3, 7. Obverse of zoarial fragments with slightly different meshwork characteristics. PD.4689, ×5·0; and PD.4690 ×7·1, respectively.

FIG. 4. Obverse side showing normal branches passing distally into sterile lateral processes. PD.4691. ×7·2.

FIGS 5, 8. Obverse of meshwork showing localized development of thick, striated, secondary skeleton. PD.4692, ×8·0; and PD.4693, ×7·0.

FIG. 6. Reverse of zoarial fragment showing branches passing distally into stout, barbed, lateral spines. PD.4694. ×5·4.

FIG. 9. Detail of obverse surface. PD.4689. ×18·3.



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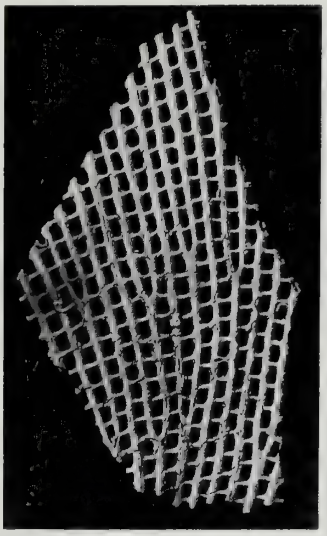

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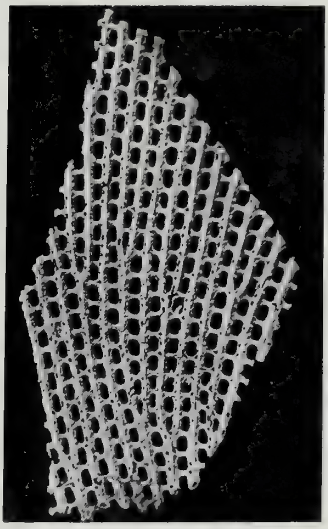

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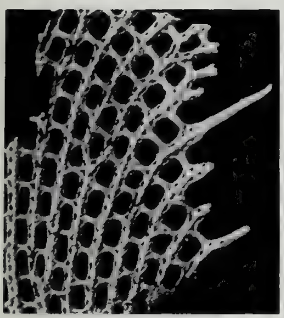

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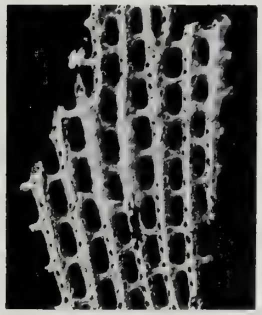

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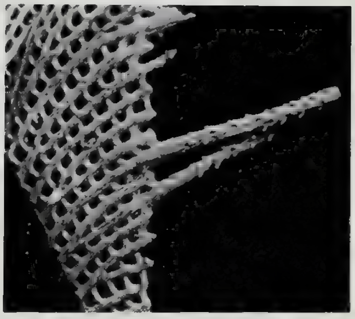

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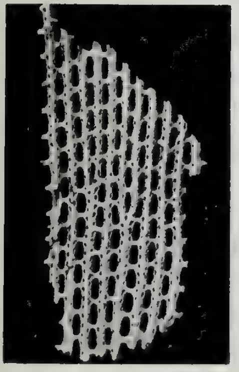

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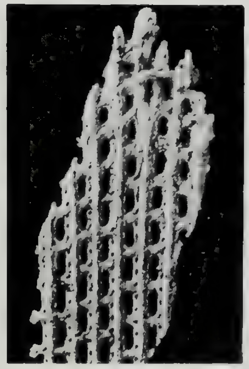

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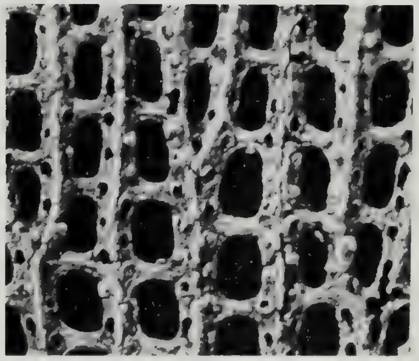

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PLATE 4

Fenestella modesta Ulrich

FIGS 1, 2, 4, 6. Obverse of zoarial fragments illustrating variation in meshwork pattern. PD.4696, ×6·6; PD.4698, ×5·0; PD.4695, ×6·8; and PD.4697, ×6·4, respectively.

FIG. 3. Detail of obverse surface. ×25·0.

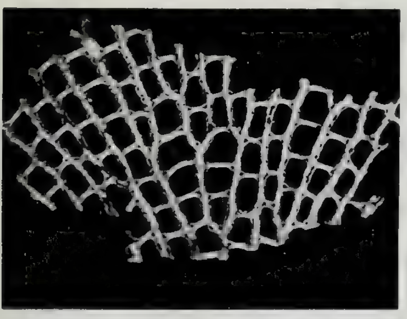
FIG. 5. Reverse of zoarial fragment. PD.4695. ×6·8.

Fenestella hemispherica M'Coy

FIG. 7. Obverse of zoarial fragment. PD.4699. ×13·5.

FIG. 8. Reverse surface showing uniserial nodes along mid-lines of branches. PD.4704. ×6·3.

FIG. 9. Large fragment showing typical meshwork pattern. PD.4701. ×4·7.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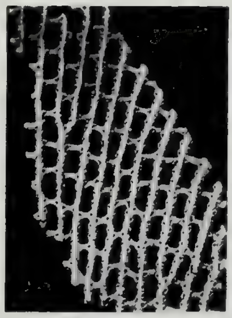
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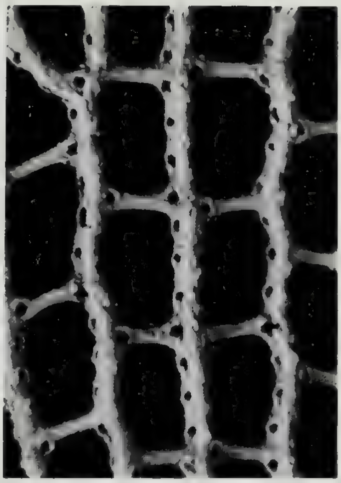
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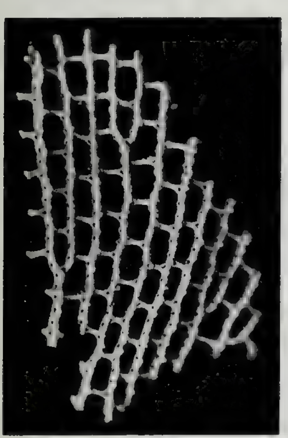
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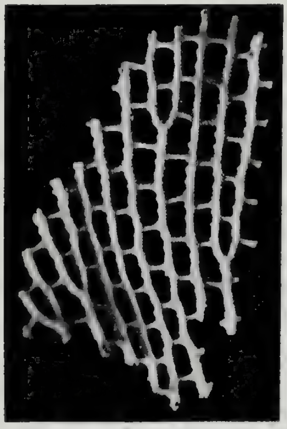
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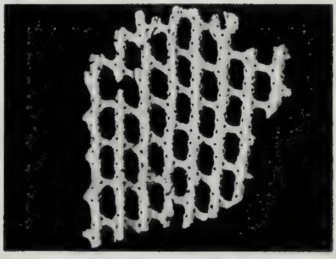
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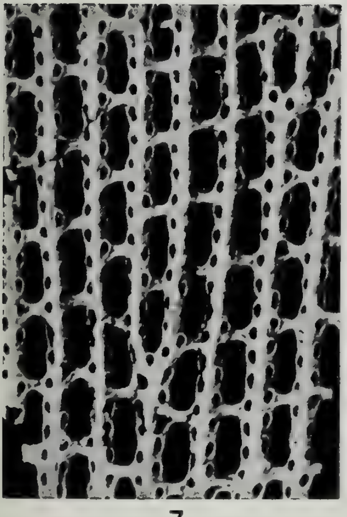
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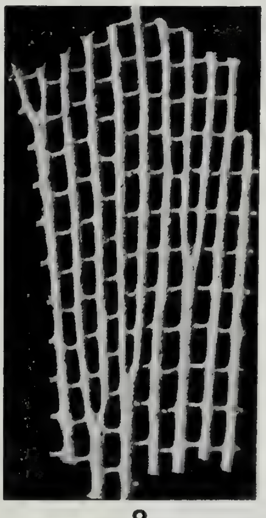
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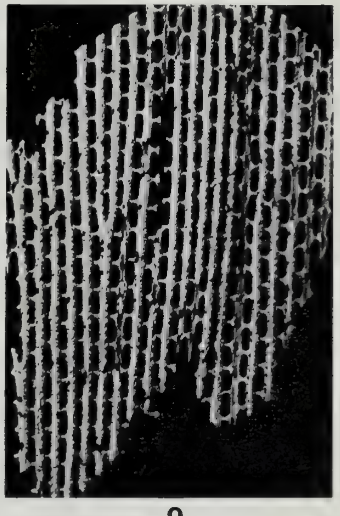
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PLATE 5

Fenestella hemispherica M'Coy

FIGS 1, 2. Obverse surface of zoarial fragments. PD.4700, ×15·0; and PD.4702, ×6·6.

FIG. 3. Reverse side showing nodes. PD.4699. ×5·8.

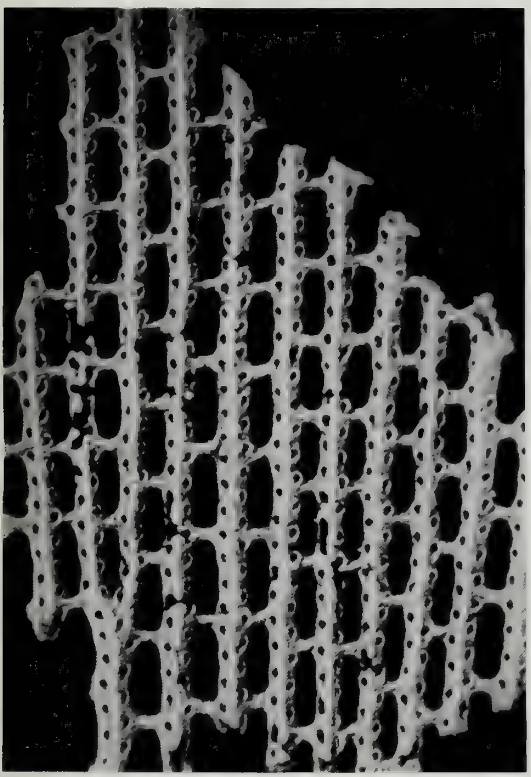
FIG. 4. Obverse of meshwork showing characteristic mode of branch division. PD.4704. ×13·8.

Fenestella parallela Hall

FIG. 5. Reverse of zoarial fragment showing striated pattern. PD.4710. ×7·3.

FIGS 6, 8, 9. Obverse surfaces showing meshwork characteristics. PD.4707 to PD.4709 ×7·0; ×7·0; ×9·7, respectively.

FIG. 7. Detail of obverse side. PD.4708. ×14·5.



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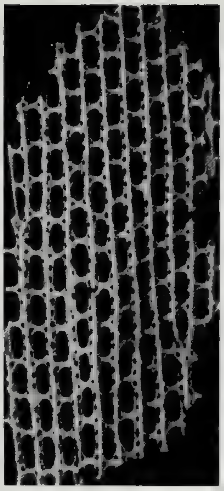

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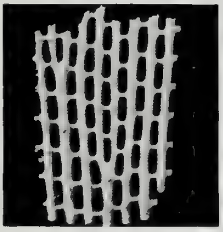

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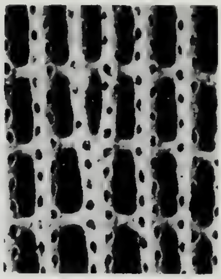

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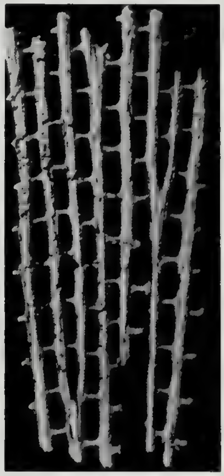

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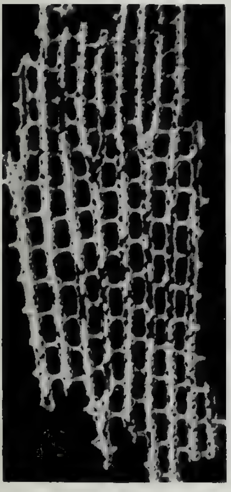

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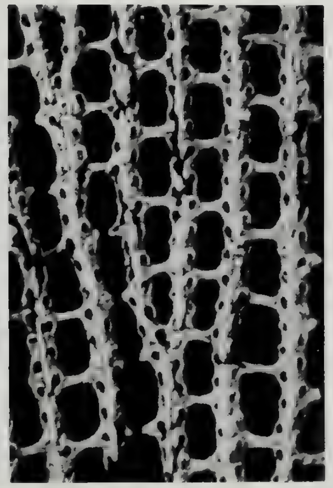

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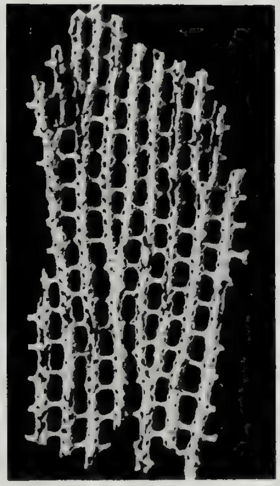

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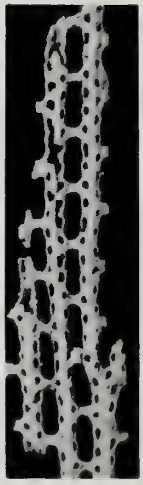

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PLATE 6

Fenestella rudis Ulrich ***multinodosa*** subsp. nov.

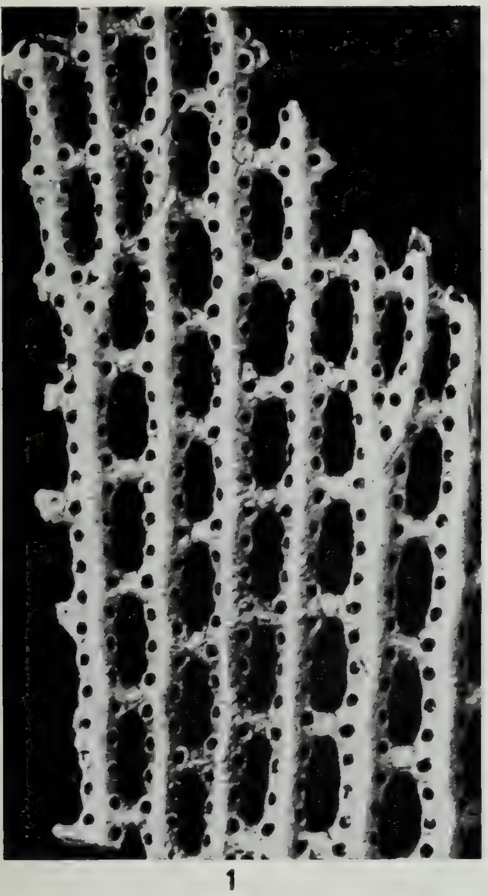
FIG. 1. Detail of obverse of a zoarial fragment. × 14·2.

FIG. 2. Obverse of meshwork with localized presence of thick, secondary skeleton which has coated branch surfaces and reduced or sealed zooecial apertures. PD.4714 (paratype). × 8·8.

FIG. 3. Reverse side of zoarial fragment. PD.4714 (paratype). × 8·2.

FIGS 4, 6, 7. Obverse of fragments showing slight differences of meshwork pattern. PD.4713 (paratype), × 5·0; PD.4716 (paratype), × 7·4; and PD.4712 (holotype), × 5·0.

FIG. 5. Obverse of partly silicified fragment showing hemi-hexagonal zooecial chambers. PD.4715 (paratype). × 7·9.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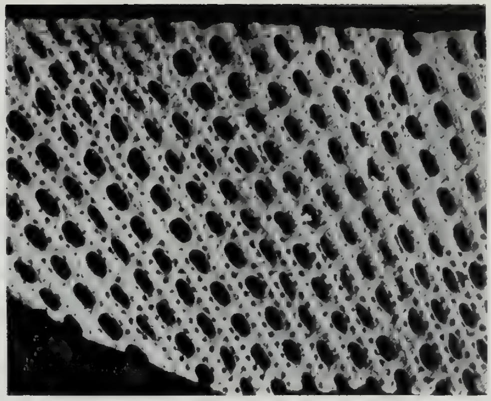
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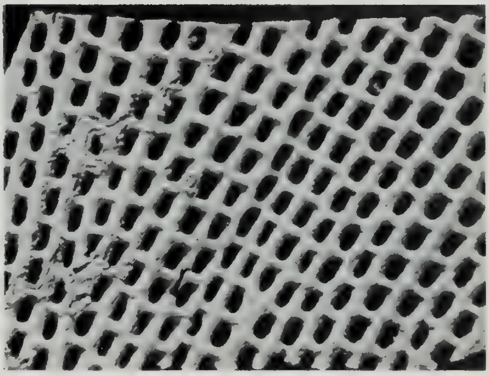
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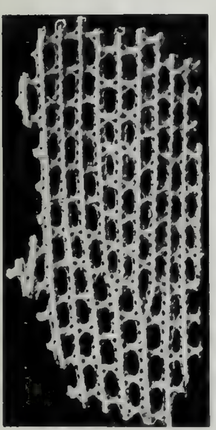
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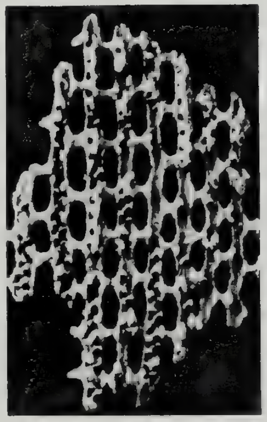
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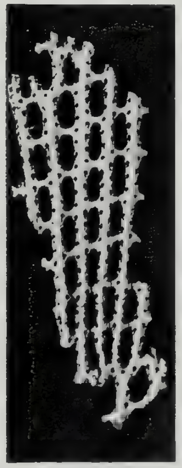
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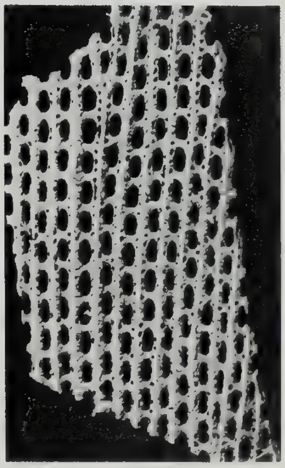
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PLATE 7

Fenestella plebeia M'Coy

FIG. 1. Obverse of zoarial fragment showing meshwork pattern. PD.4719. ×3·6.

FIGS 2, 3. Detail of obverse surface. Fig. 3, from proximal part of colony shows thick secondary skeletal envelope. Minute punctae along branch medial lines are carinal node bases. PD.4719, ×11·4; and PD.4717, ×11·3, respectively.

FIG. 4. Obverse of zoarial fragment from proximal part of colony. PD.4717. ×4·5.

FIG. 5. Obverse of partly silicified fragment showing triangular zooecial chambers. PD.4718. ×6·0.

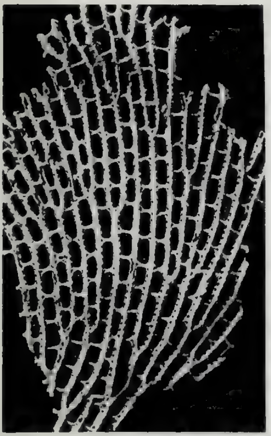
FIG. 6. Zoarial fragment with inflated peristomes projecting into fenestrules. PD.4721. ×6·4.

FIG. 7. Reverse surface of zoarial fragment. PD.4717. ×4·5.

Fenestella cf. **arthritica** Phillips

FIG. 8. Detail of obverse surface. PD.4722. ×15·0.

FIG. 9. Large zoarial fragment giving an impression of the colonial growth form. PD.4728. ×2·9.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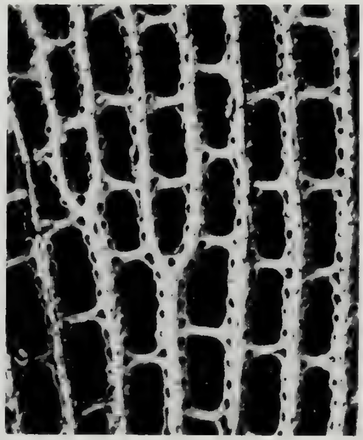
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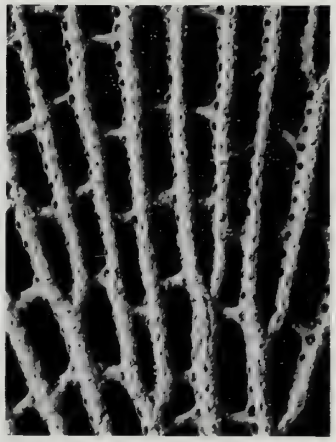
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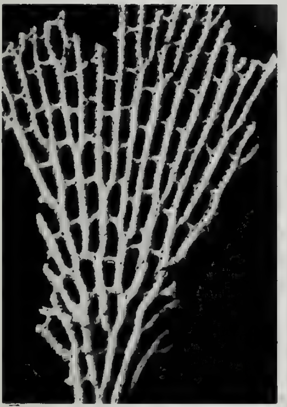
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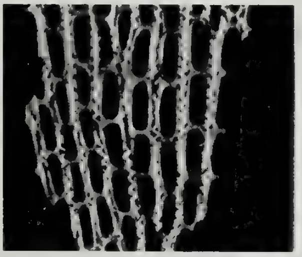
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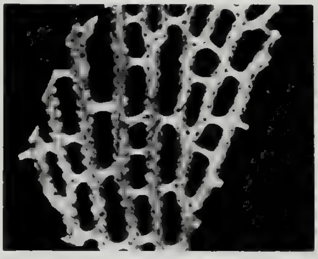
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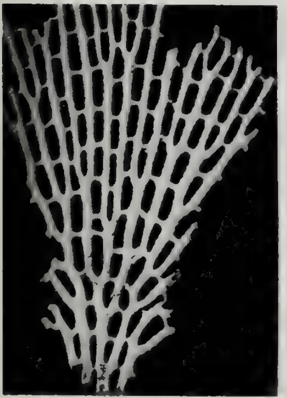
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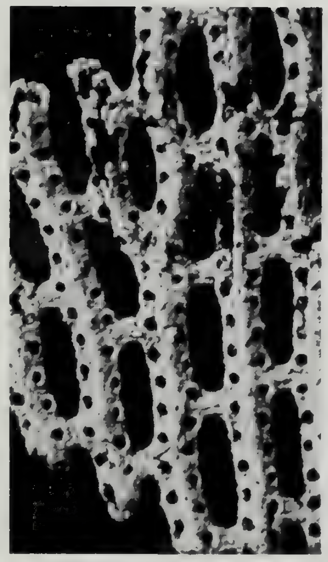
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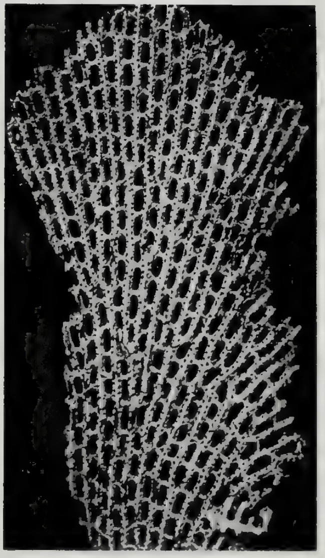
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PLATE 8

Fenestella cf. ***arthritica*** Phillips

Figs 1, 3, 4. Obverse of zoarial fragments showing characteristics of meshwork pattern. Stout carinal nodes are visible along proximal part of middle branch in Fig. 3. PD.4727, ×3·9; PD.4726, ×5·0; and PD.4724, ×5·1. respectively.

Fig. 2. Reverse surface of meshwork. PD.4727. ×3·9.

Fenestella praemagna Shulga-Nesterenko

Fig. 5. Proximal part of a colony with basal holdfast and lateral supporting struts. PD.4732. ×5·0.

Fig. 6. Strong carinal nodes, which divide at their distal ends, originate along the obverse mid-lines of branches. PD.4735. ×5·1.

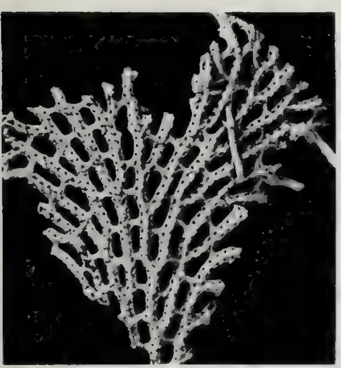
Fig. 7. Proximal part of a colony attached to a *Penniretepora* branch. PD.4733. ×4·7.

Fig. 8. Obverse of colony showing basal holdfast and supporting processes. PD.4734. ×10·4.

Fig. 9. Detail of obverse. PD.4731. ×14·0.

Fig. 10. Reverse side of zoarial fragment. PD.4730. ×6·1.

Fig. 11. Obverse of proximal part of an old colony, with thick secondary skeletal cover. PD.4729. ×7·0.



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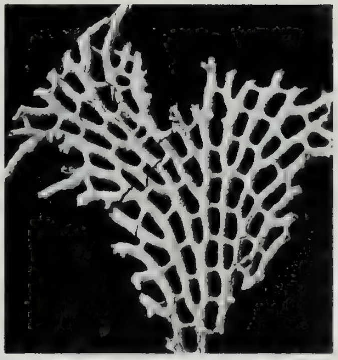

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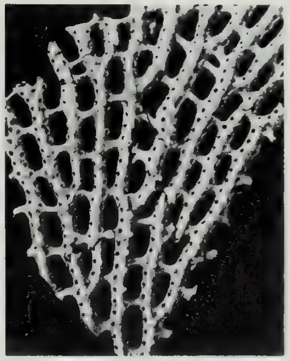

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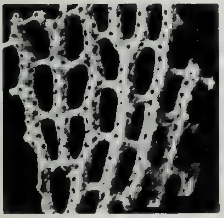

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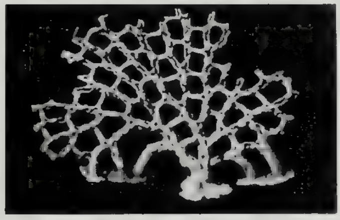

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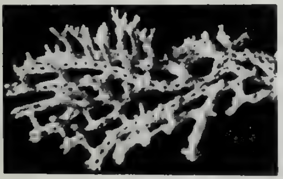

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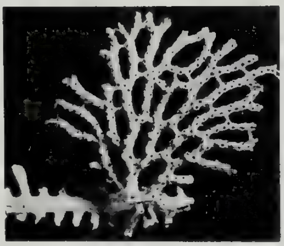

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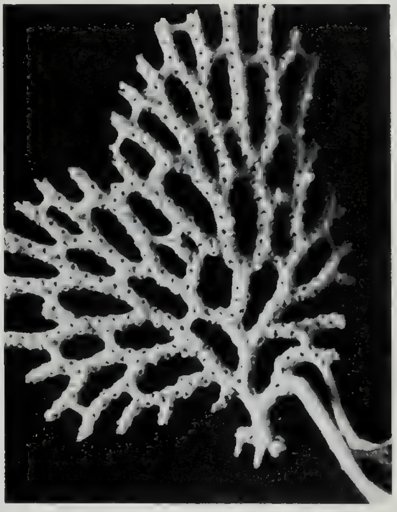

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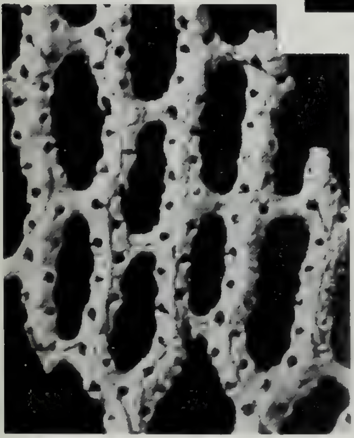

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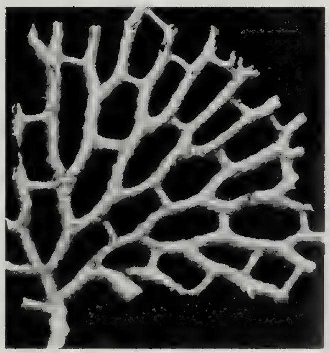

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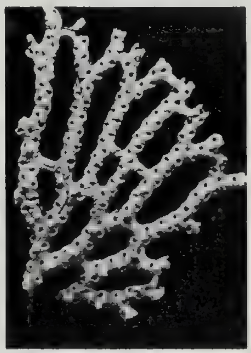

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PLATE 9

Fenestella fanata Whidborne ***carrickensis*** subsp. nov.

FIG. 1. Obverse of meshwork showing characteristic pattern at branch division. PD.4736 (holotype). ×10·1.

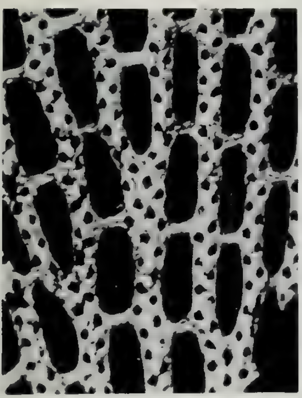
FIG. 2. Zoarial fragment with stout lateral spine developed as a branch continuation. PD.4737 (paratype). ×3·5.

FIGS 3, 5, 7, 8. Obverse of zoarial fragments, showing general meshwork characteristics. Specimen shown in Fig. 3 (×3·9) is not preserved. The others are numbered: PD.4738 (paratype), ×5·0; PD.4739 (paratype), ×3·8; and PD.4736, ×3·5, respectively.

FIG. 4. Zoarial fragment with ovicells visible in the distal part. PD.4740 (paratype). ×3·5.

FIG. 6. Reverse side of a fragment, showing evidence of damage and subsequent repair during the life of the colony. PD.4741. ×3·3.

FIG. 9. Detail of obverse surface. PD.4742 (paratype). ×9·9.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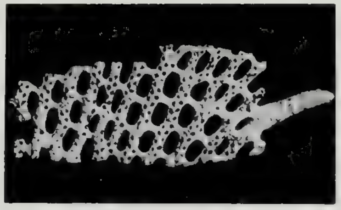
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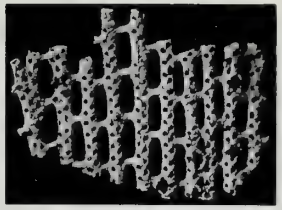
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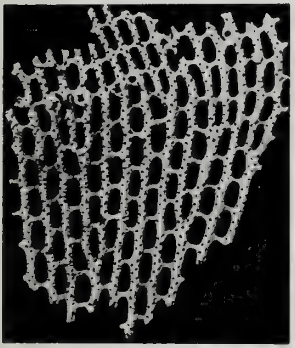
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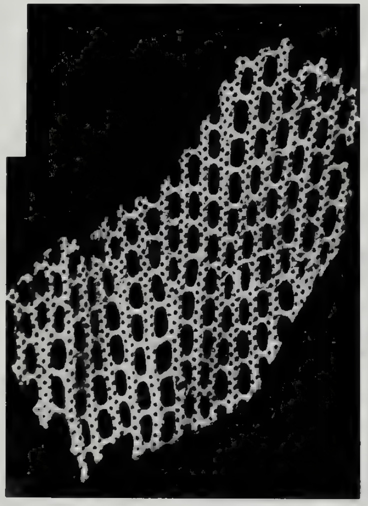
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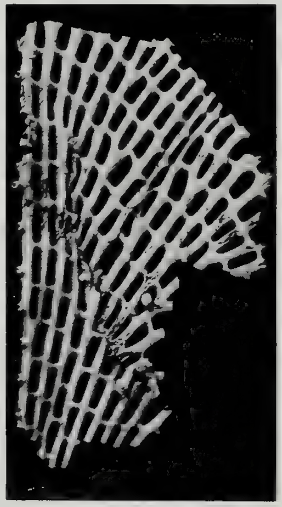
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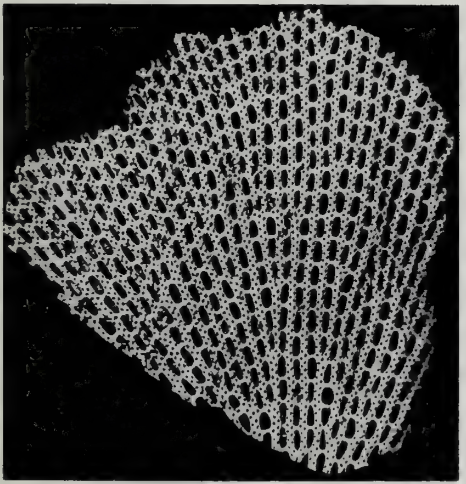
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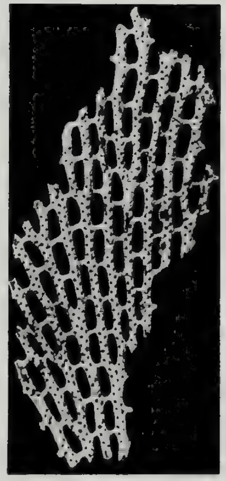
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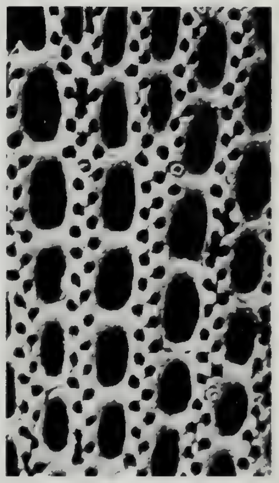
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PLATE 10

***Fenestella* cf. *spinacristata* Moore**

FIG. 1. Large zoarial fragment showing overall meshwork pattern. PD.4743. ×3·8.

FIG. 2. Reverse surface of meshwork. PD.4746. ×5·0.

FIG. 3. Detail of obverse side. PD.4743. ×9·5.

FIG. 4. Proximal part of a colony with holdfast attached to a *Penniretepora* branch. PD.4747. ×6·1.

FIG. 5. Obverse of zoarial fragment. PD.4744. ×7·1.

FIG. 6. Fragment bearing evidence of structural damage and repair during the life of the colony. PD.4750. ×4·5.

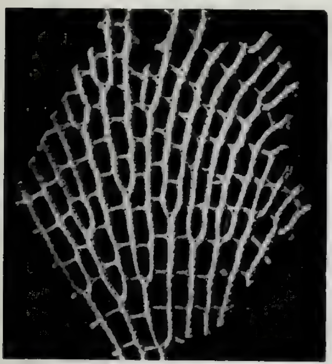
***Fenestella* cf. *funicula* Ulrich**

FIG. 7. Reverse side of fragment from proximal part of a colony, showing a stout spine developed from obverse mid-line of a branch. PD.4758. ×5·5.

FIG. 8. Obverse of a zoarial fragment. PD.4751. ×5·0.

FIG. 9. Reverse side of above. PD.4751. ×5·0.

FIG. 10. Fragment from proximal part of an old colony showing thick secondary skeletal encrustation. PD.4759. ×2·9.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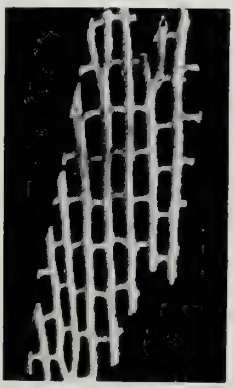
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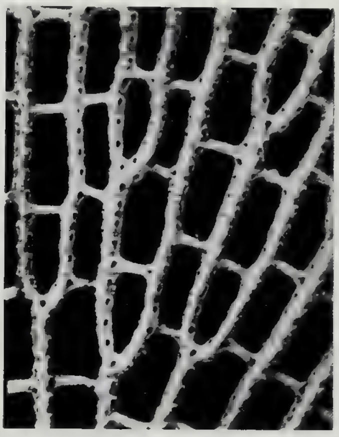
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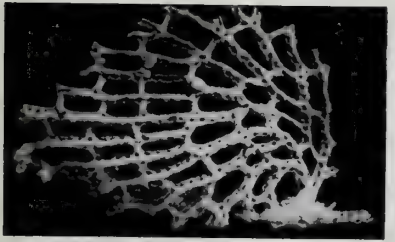
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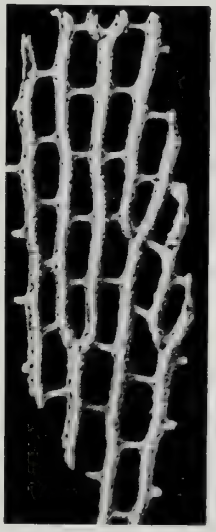
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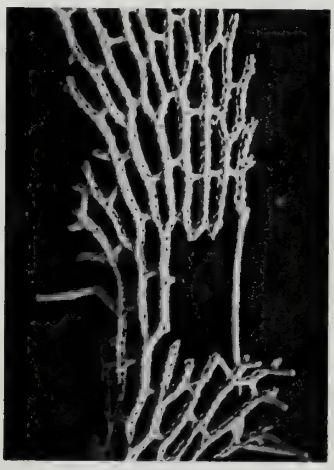
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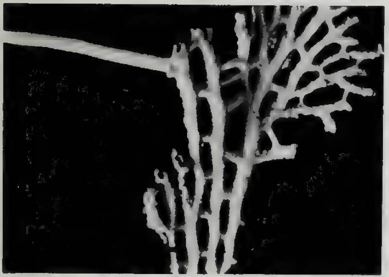
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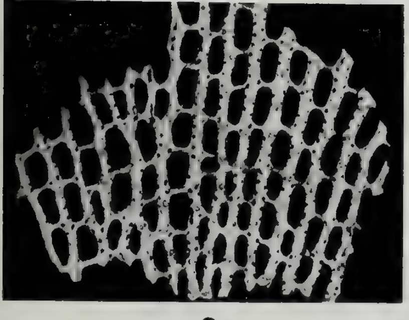
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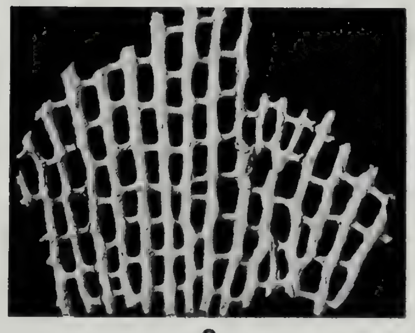
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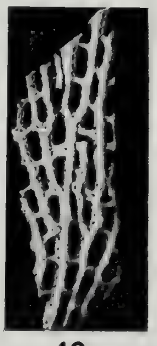
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PLATE 11

Fenestella cf. ***funicula*** Ulrich

FIG. 1. Obverse of zoarial fragment showing ovicells in the distal part. PD.4759. ×4·3.

FIGS 2, 3. Obverse surfaces showing general meshwork characteristics. PD.4753, ×6·8; and PD.4755, ×7·0.

FIG. 4. Obverse surface of meshwork with strong carinal nodes. PD.4756. ×4·0.

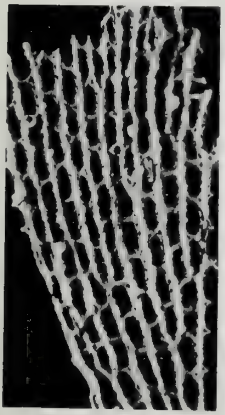
Fenestella filistriata Ulrich

FIGS 5, 7, 9. Obverse of zoarial fragments showing meshwork pattern. PD.4763, ×5·3; PD.4761 ×3·8 and PD.4762, ×5.0, respectively.

FIG. 6. Reverse surface. PD.4763. ×5·5.

FIG. 8. Reverse of zoarial fragment showing longitudinal 'striae' and hemi-hexagonal bases of zooecial chambers. PD.4764. ×7·0.

FIG. 10. Detail of obverse. PD.4761. ×12·2.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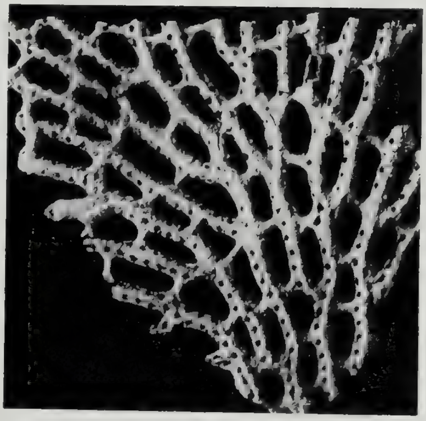
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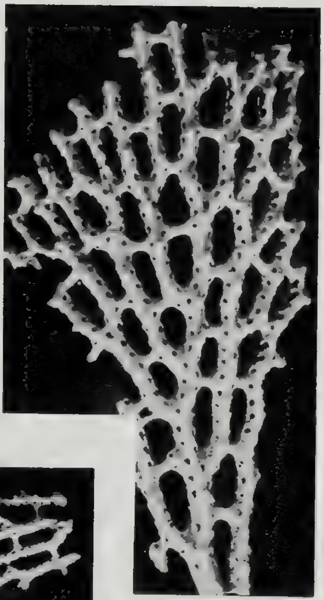
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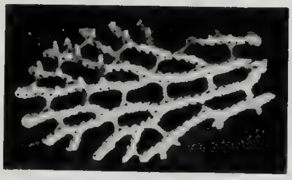
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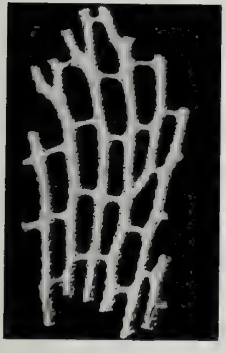
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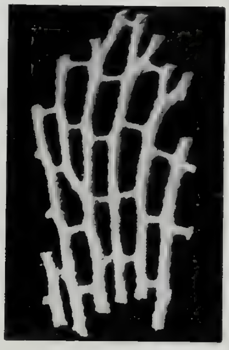
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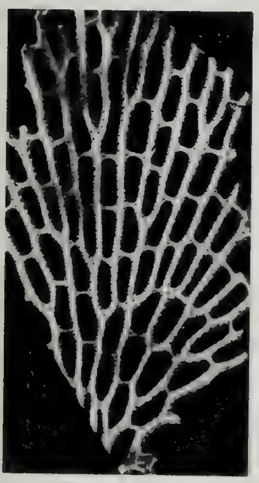
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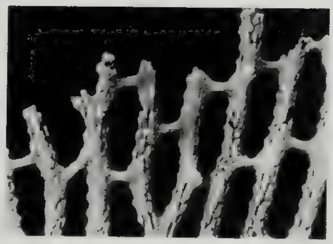
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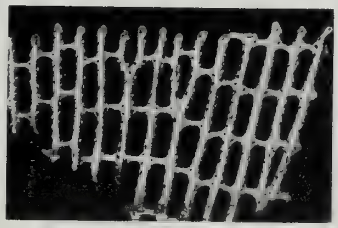
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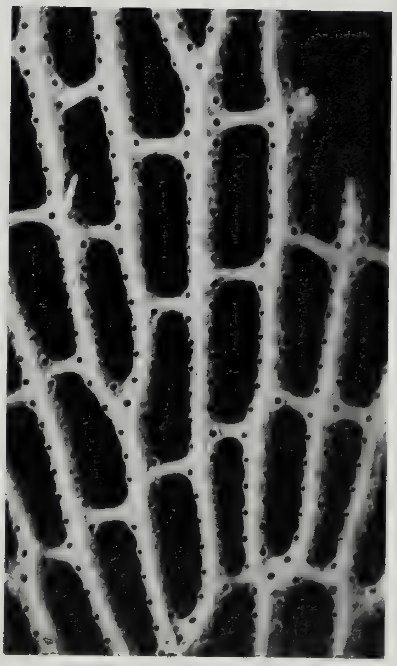
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PLATE 12

Fenestella cf. ***filistriata*** Ulrich

FIG. 1. General view of obverse side of a zoarial fragment. PD.4761. ×5·2.

Fenestella subspeciosa Shulga-Nesterenko

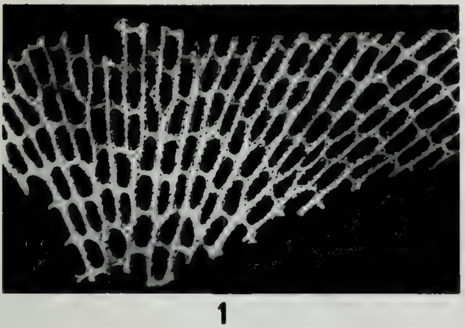
FIG. 2. Reverse surface. PD.4766. ×5·7.

FIGS 3, 4, 5. Obverse of zoarial fragments showing general meshwork characteristics. PD.4765, ×5·0; PD.4769, ×4·0; and PD.4767, ×5·6.

FIG. 6. Obverse at higher magnification, showing prominent cowl-like peristomes indenting fenestrule margins. PD.4766. ×5·2.

FIG. 7. Reverse of zoarial fragment showing a stout spine which resulted from continued growth from an abnormally directed dissepiment. This spine later re-united with the meshwork, as shown. ×7·2.

FIG. 8. Obverse of above fragment showing a local concentration of secondary skeletal tissue where the aberrant spine (coming from below) rejoined the meshwork. ×7·2.



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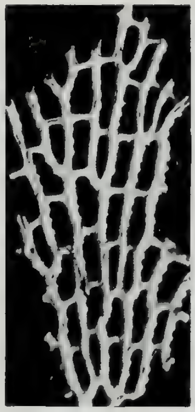

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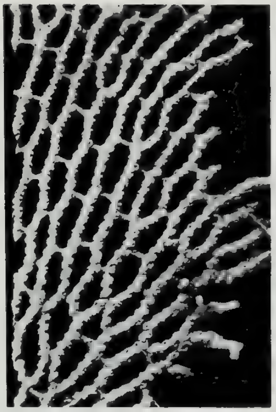

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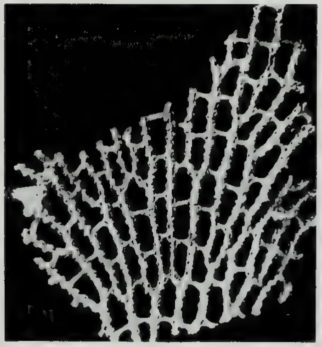

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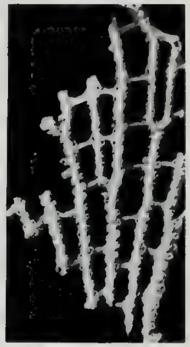

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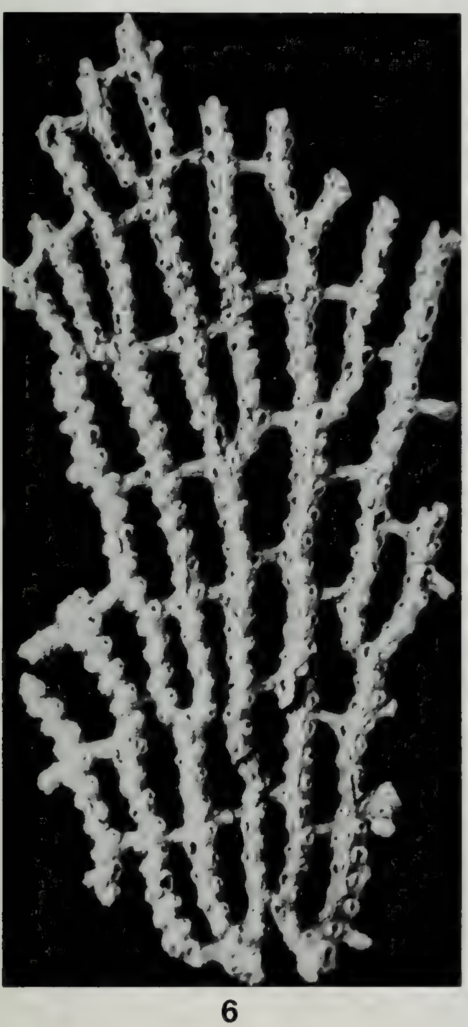

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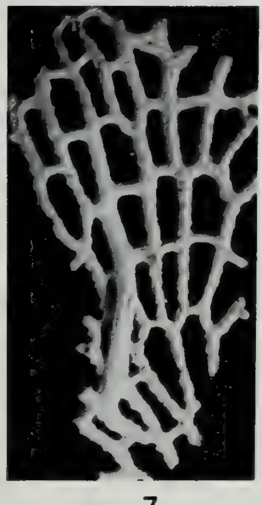

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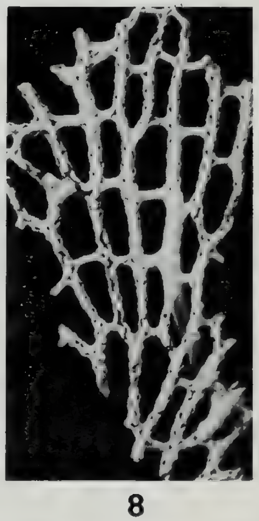

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PLATE 13

Fenestella pseudovirgosa Nikiforova

FIG. 1. Detail of obverse. PD.4770. × 15·0.

FIG. 2. Reverse side of meshwork. PD.4771. × 2·9.

FIG. 3. Zoarial fragment showing general meshwork characteristics. PD.4770. × 5·0.

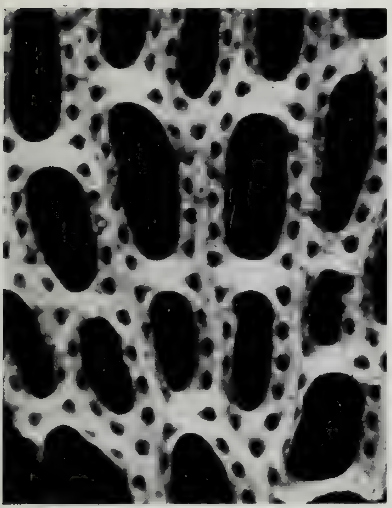
FIG. 4. The stout spine developed from a branch end in the distal part of this specimen grew back and re-united with the reverse side of the meshwork. PD.4772. × 3·6.

FIG. 5. This strong spine resulted from the continued growth of an abnormal dissepiment. PD.4773. × 3·7.

FIGS 6, 9. Zoarial fragments from proximal parts of colonies, showing thick deposits of secondary skeletal substance. PD.4774, × 5·6; and PD.4775, × 5·0.

FIG. 7. Obverse of fragment, showing a strong laterally directed spine. PD.4776. × 4·1.

FIG. 8. Reverse surface showing longitudinal 'striae', variably developed nodes, and the triangular base of a zooecial chamber. PD.4777. × 4·3.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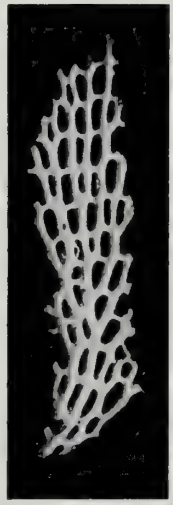
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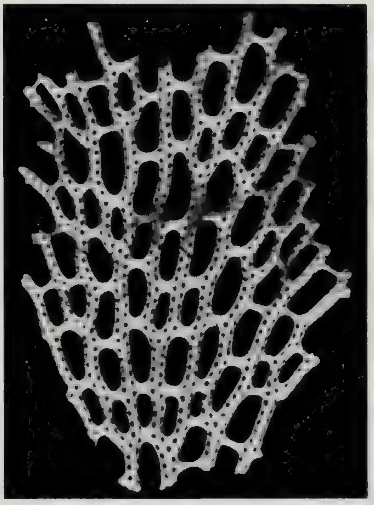
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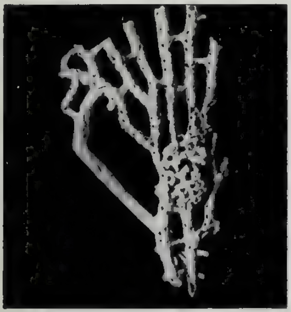
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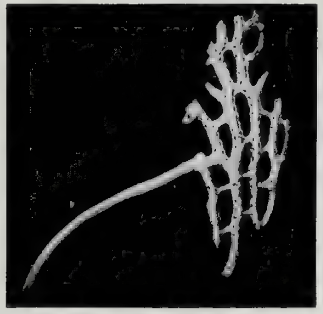
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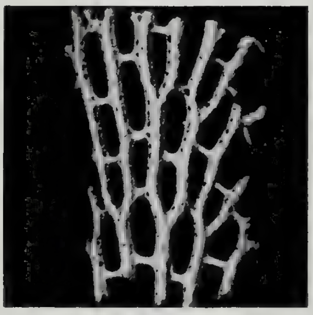
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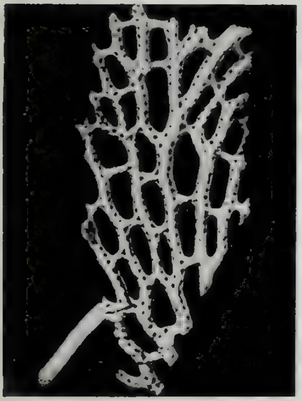
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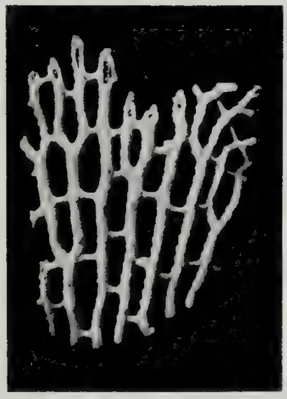
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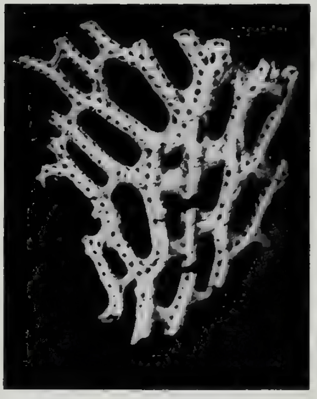
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PLATE 14

Fenestella cf. ***albida*** Hall

FIGS 1, 3. Obverse of zoarial fragments showing general meshwork characteristics. PD.4783, ×6·7; and PD.4780 ×5·0, respectively.

FIG. 2. Obverse surface showing chain-like pattern due to projection of inflated peristomes into fenestrules. PD.4781. ×6·4.

FIG. 4. Detail of obverse. PD.4780. ×15·0.

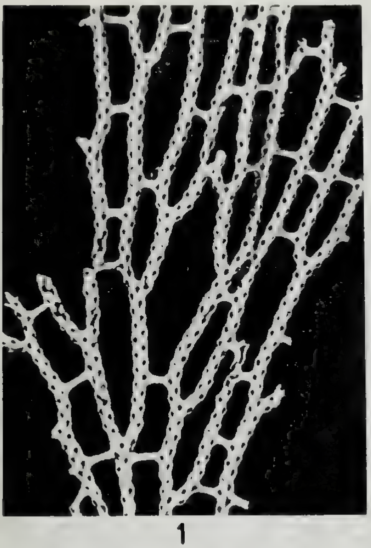
FIG. 5. Proximal part of a colony with basal attachment to a *Penniretepora* branch. PD.4779. ×3·4.

FIG. 6. Reverse side of meshwork. ×5·8.

Fenestella oblongata Koenig

FIG. 7. Obverse of a zoarial fragment. PD.4790. ×7·0.

FIG. 8. Reverse surface showing longitudinal 'striae', small nodes and the triangular base of a zooecial chamber. PD.4791. ×7·5.



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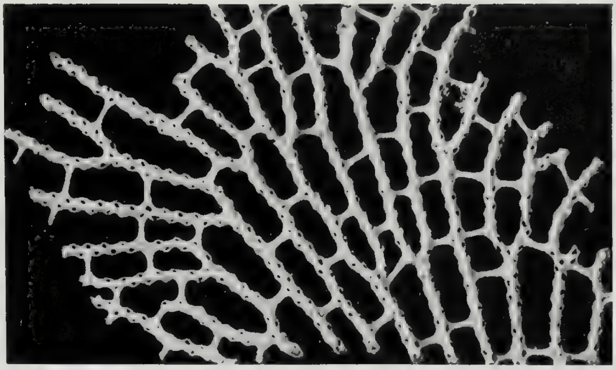

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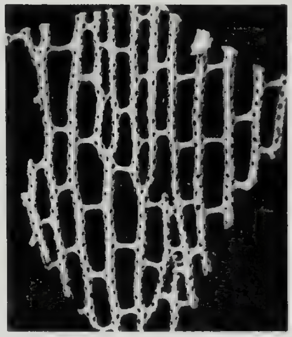

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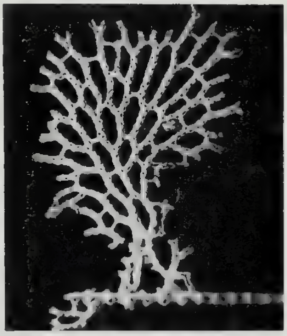

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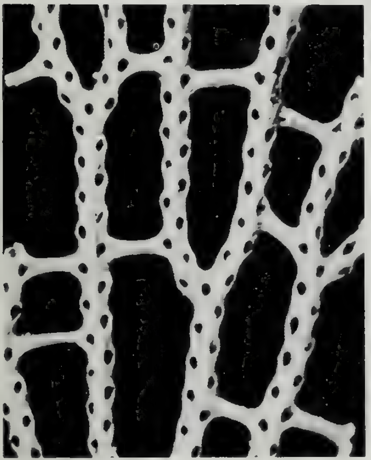

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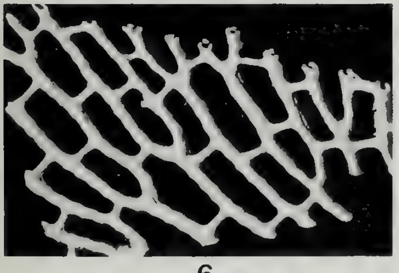

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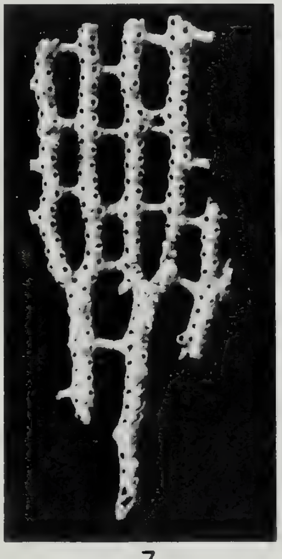

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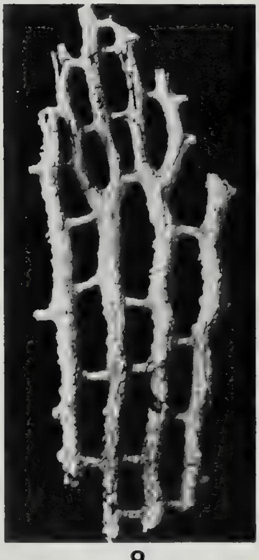

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PLATE 15

Fenestella oblongata Koenig

FIG. 1. Detail of obverse of zoarial fragment. PD.4786. ×14·8.

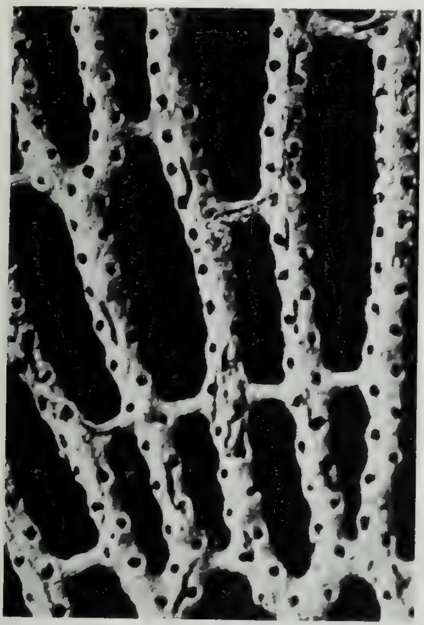
FIGS 2, 3, 4. Obverse views of fragments showing general aspect of meshwork. PD.4787, ×5·0; PD.4789, ×4·2; and PD.4786, ×6·3, respectively.

Fenestella cf. ***delicatula*** Ulrich

FIGS 5, 6. Obverse surfaces of zoarial fragments illustrating variation in meshwork characteristics. PD.4797, ×6·3; and PD.4794, ×7·0.

FIG. 7. Zoarial fragment with strong spines from the reverse side of a branch. The spines bear minute barbs. PD.4799. ×5·0.

FIG. 8. Detail of obverse side. PD.4798. ×16·0.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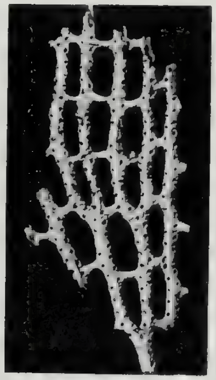
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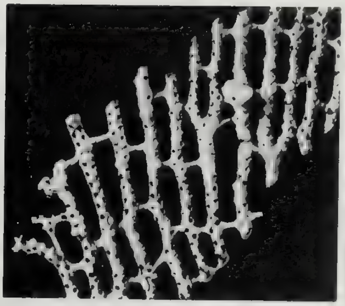
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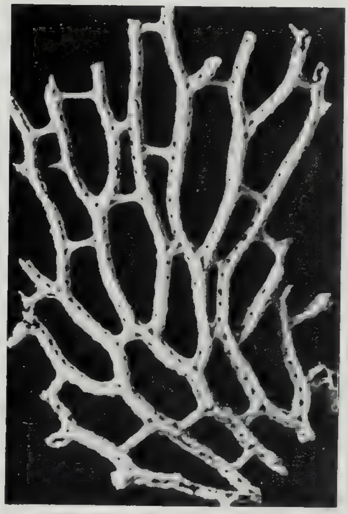
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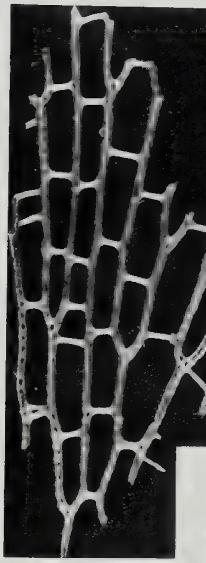
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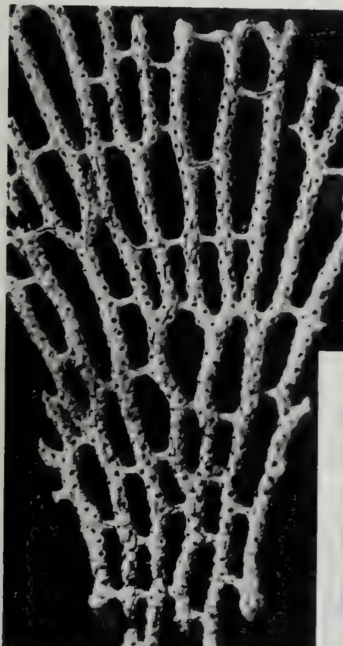
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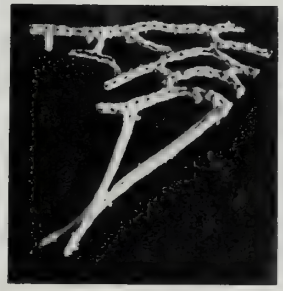
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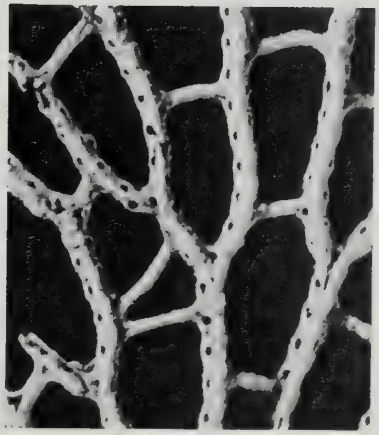
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PLATE 16

Fenestella cf. ***delicatula*** Ulrich

FIG. 1. Reverse side of meshwork. PD.4798. ×7·5.

FIG. 2. Obverse of zoarial fragment. PD.4795. ×4·8.

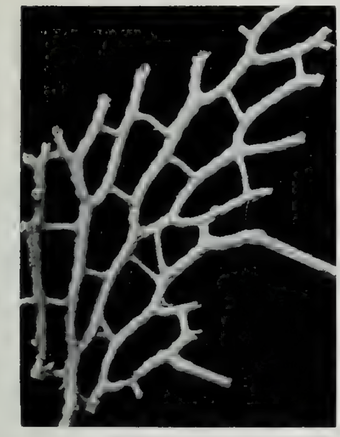
FIG. 3. Fragment with strong lateral spine developed as a branch continuation. PD.4798. ×7·5.

Fenestella polyporata (Phillips)

FIG. 4. Reverse of meshwork showing longitudinal 'striae'. PD.4802. ×7·2.

FIGS 5, 7, 8. Obverse surfaces of zoarial fragments showing general features of meshwork. PD.4805, ×7·0; PD.4802, ×3·7; and PD.4804, ×5·0, respectively.

FIG. 6. Detail of obverse. PD.4804. ×14·9.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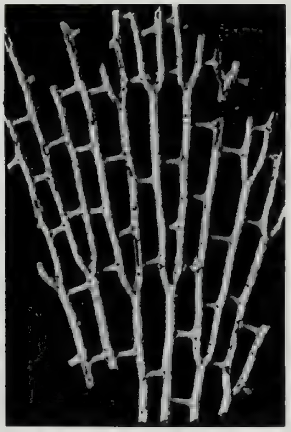
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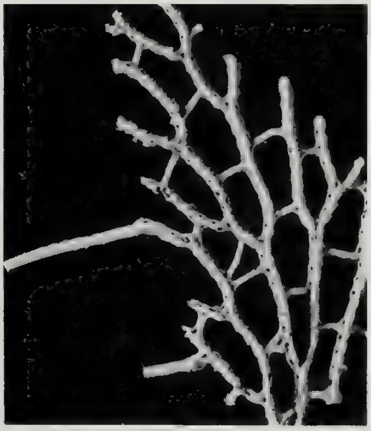
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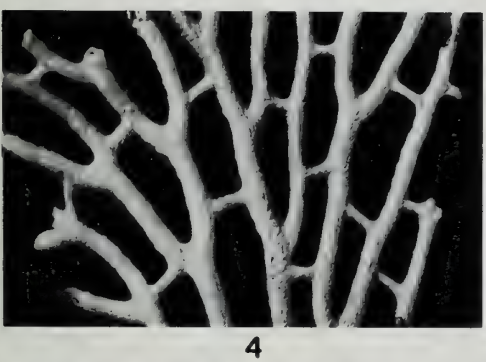
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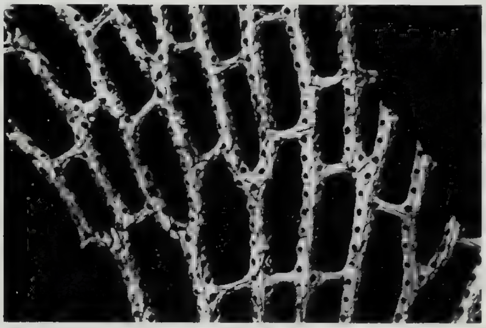
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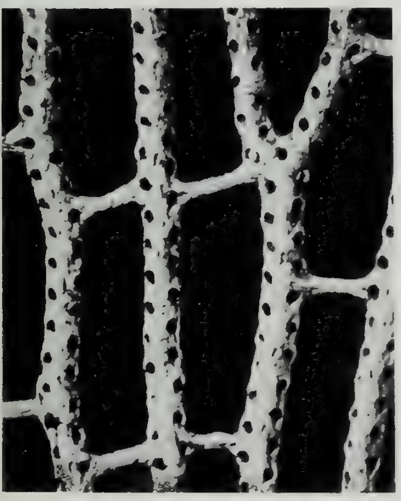
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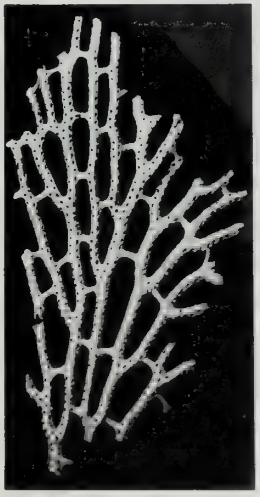
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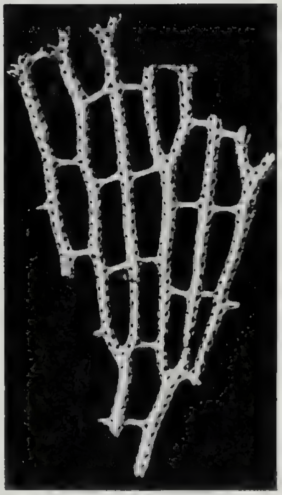
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PLATE 17

Fenestella polyporata (Phillips)

FIG. 1. Obverse of zoarial fragment. PD.4803. ×7·1.

Fenestella irregularis Nekhoroshev

FIGS 2, 5. Obverse of zoarial fragments, showing meshwork features. PD.4808 ×7·1; and PD.4811, ×3·9, respectively.

FIG. 3. Detail of obverse. PD.4810. ×13·0.

FIG. 4. Reverse side of zoarial fragment. PD.4809. ×7·5.

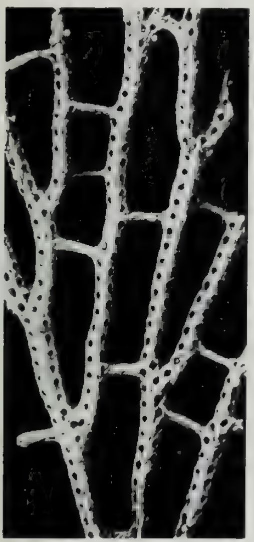
FIG. 6. Obverse of incompletely silicified fragment showing casts of zooecial chambers. PD.4813. ×8·5.

FIG. 7. Oblique view of obverse showing strong carinal nodes. PD.4812. ×4·5.

Levifenestella undecimalis (Shulga-Nesterenko)

FIG. 8. Reverse surface with longitudinal 'striae' and grooves excavated by ramifying *Condranema* (ctenostome) stolons. PD.4815. ×5·0.

FIG. 9. Detail of obverse. PD.4816. ×16·0.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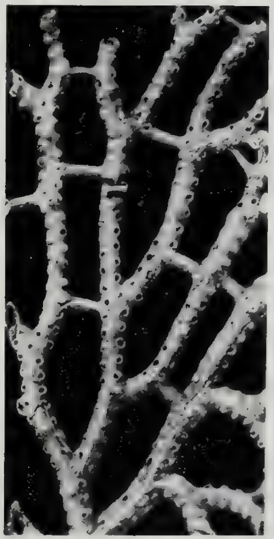
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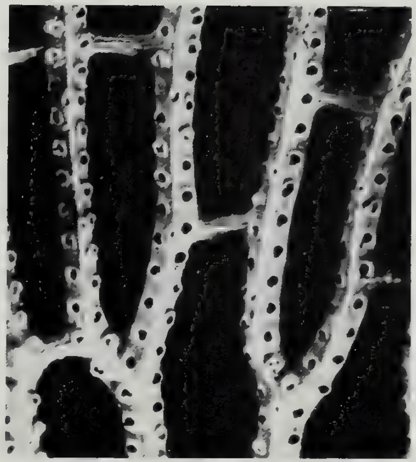
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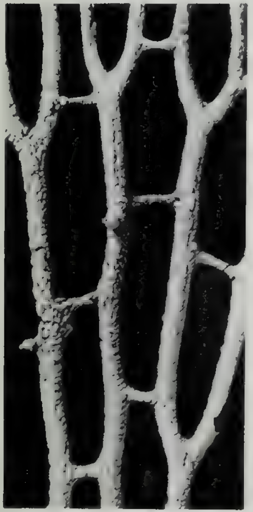
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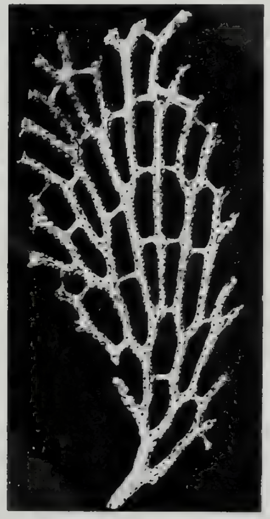
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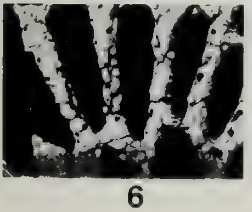
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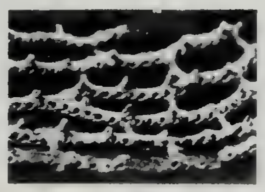
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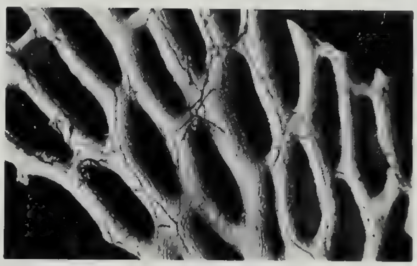
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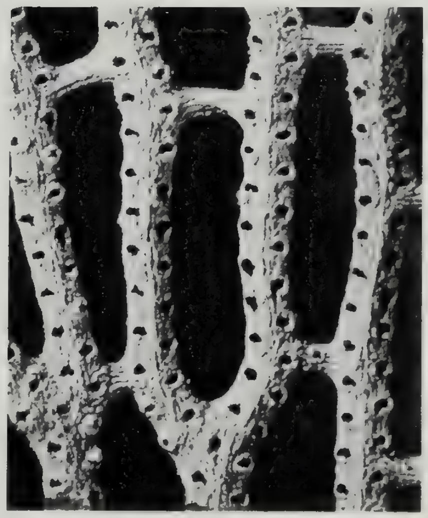
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PLATE 18

Levifenestella undecimalis (Shulga-Nesterenko)

Figs 1, 2, 4. Obverse surfaces of zoarial fragments. PD.4817, ×6·6; PD.4814, ×4·0; and PD.4820, ×6·2, respectively.

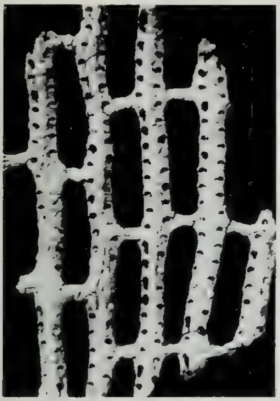
Fig. 3. Reverse of meshwork showing closely spaced longitudinal 'striae'. PD.4816. ×7·3.

Fig. 5. Obverse of large zoarial fragment which gives an idea of the colonial growth form. PD.4818. ×2·3.

Minilya plummerae (Moore)

Fig. 6. Small fragment with a stout, barbed spine developed from the reverse surface. PD.4827. ×6·5.

Figs 7, 8. Obverse of zoarial fragments showing general aspect of meshwork. PD.4825, ×6·0; and PD.4824, ×7·5, respectively.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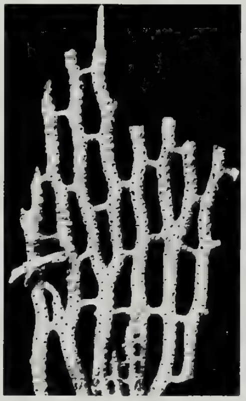
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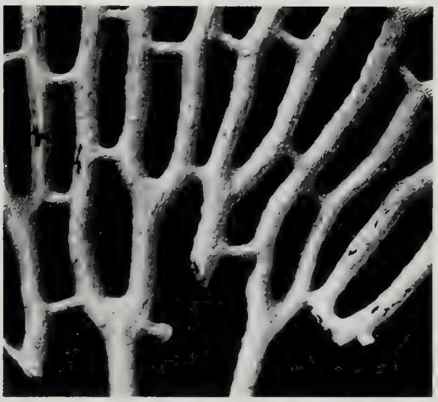
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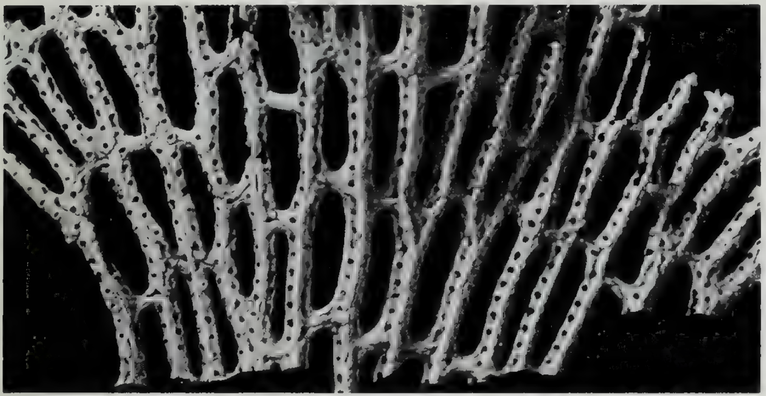
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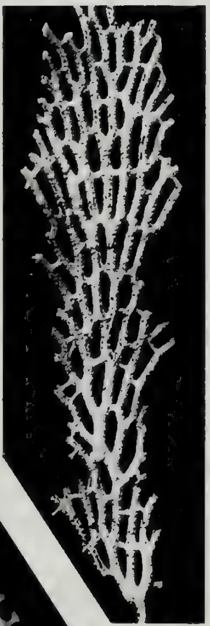
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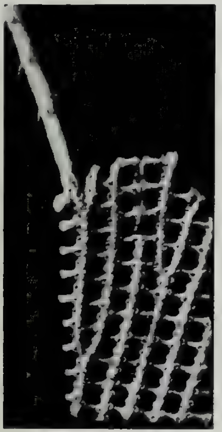
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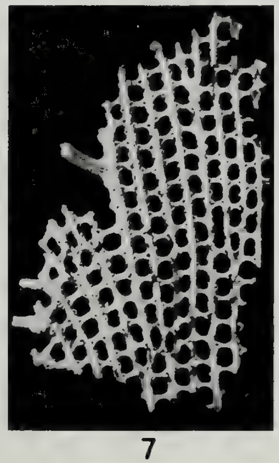
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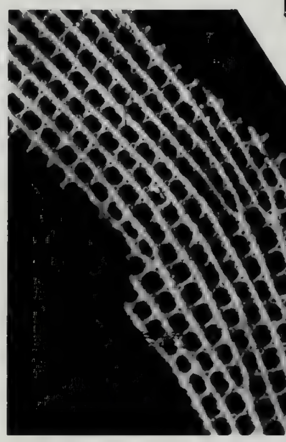
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PLATE 19

Minilya plummerae (Moore)

FIG. 1. Detail of obverse of meshwork. Positions of carinal nodes are indicated on a part of one branch. PD.4823. ×22·0.

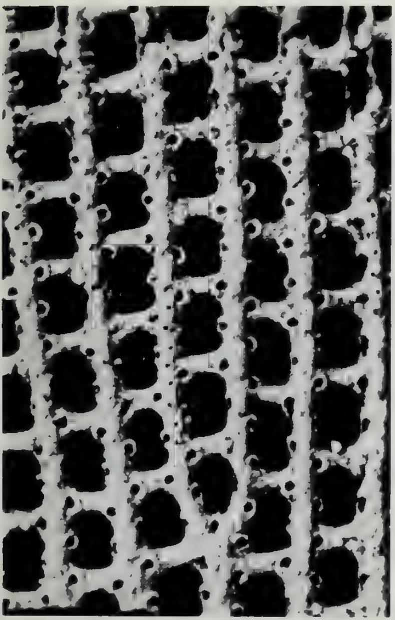
FIGS 2, 4. Obverse of zoarial fragments, showing general meshwork characteristics. PD.4823, ×6·6; and PD.4822, ×5·0, respectively.

FIG. 3. Reverse surface. PD.4822. ×5·0.

Minilya binodata (Condra)

FIGS 5, 7. Obverse of zoarial fragments. PD.4829, ×7·3; and PD.4848, ×8·5.

FIG. 6. Reverse surface. PD.4828. ×5·8.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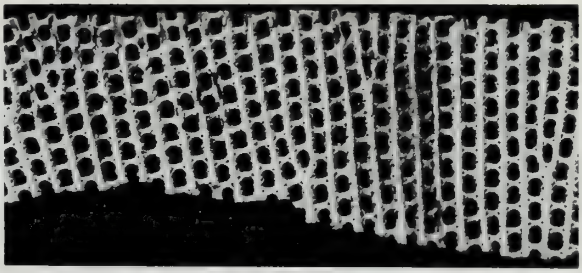
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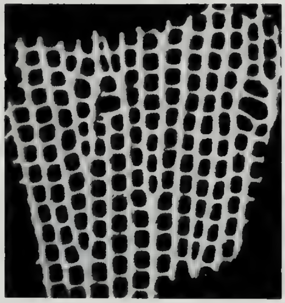
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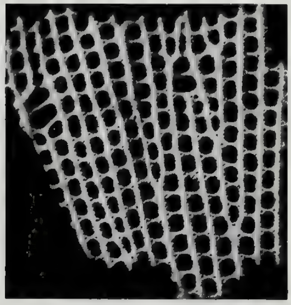
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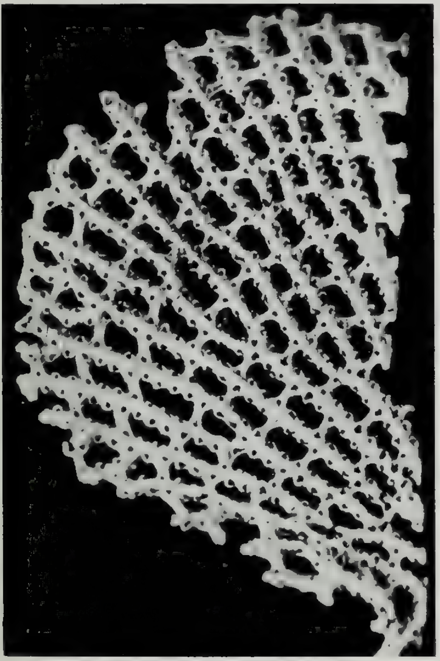
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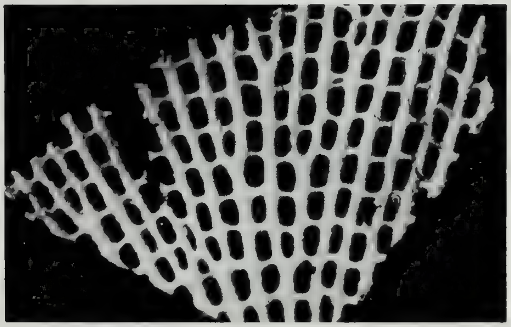
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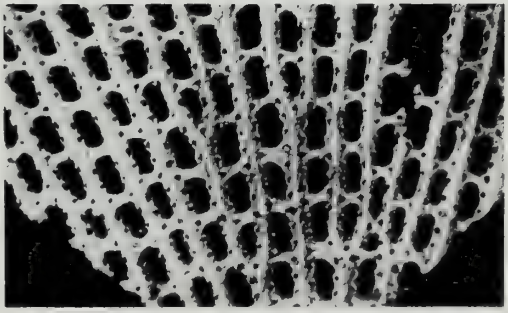
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PLATE 20

Minilya binodata (Condra)

Fig. 1. Detail of obverse, with the positions of some carinal nodes indicated. PD.4828. ×16·5.

Minilya oculata (M'Coy)

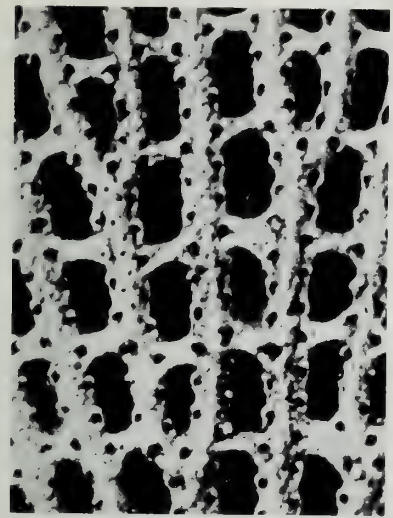
Fig. 2. A fragment from the proximal part of an old colony, with thick secondary skeletal investment. PD.4833. ×6·2.

Fig. 3. Detail of obverse showing the biserial arrangement of carinal nodes. PD.4838. ×17·5.

Figs 4, 6, 8. Obverse of zoarial fragments, showing meshwork pattern and growth habit. PD.4834, ×5·0; PD.4837, ×6·4; and PD.4835. ×6·9, respectively.

Fig. 5. Reverse side of zoarial fragment. PD.4839. ×6·5.

Fig. 7. Proximal part of a colony with holdfast attached to a *Rhabdomeson* fragment. PD.4832. ×3·9.



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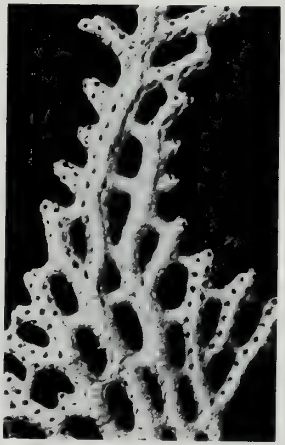

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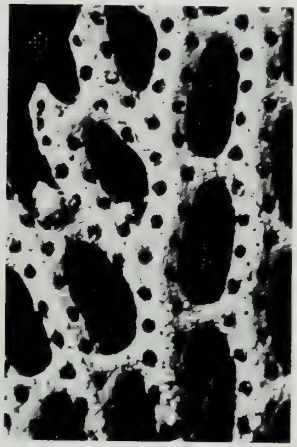

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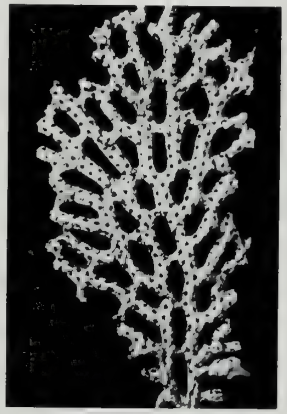

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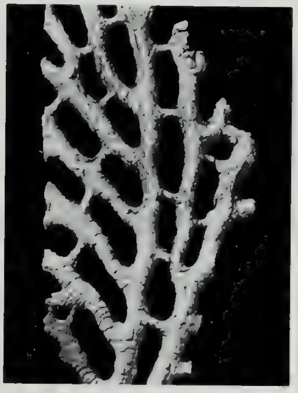

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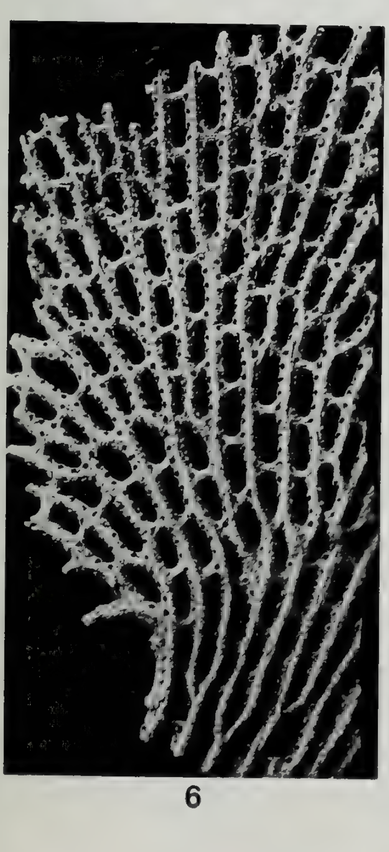

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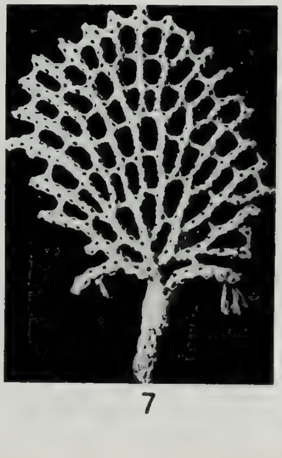

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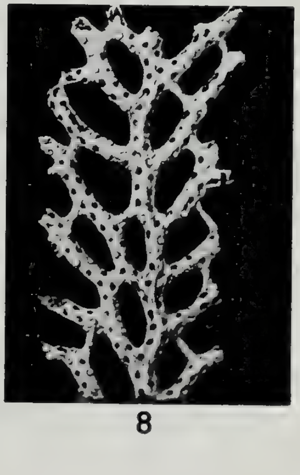

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PLATE 21

Ptiloporella varicosa (M'Coy)

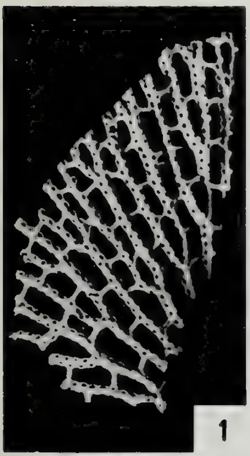
FIGS 1, 2, 3, 6, 7. Obverse of zoarial fragments showing prominent development of primary and secondary branches. PD.4840 to PD.4844 inclusive, ×4·0; ×4·7; ×5·0; ×2·6; ×2·7, respectively.

FIG. 4. This specimen, with a midrib and symmetrically placed lateral branches, resembles *Ptylopora* M'Coy in its growth pattern. PD.4845. ×4·6.

FIG. 5. Small fragment with strong spinose structures which originate on the obverse midline. PD.4846. ×4·3.

FIG. 8. Reverse surface, showing the relationship between primary and secondary branches. PD.4847. × 3·9.

FIG. 9. Detail of obverse. PD.4842. ×13·5.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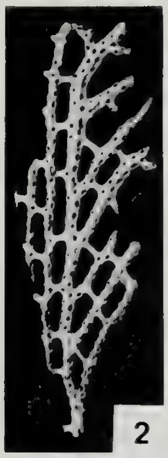
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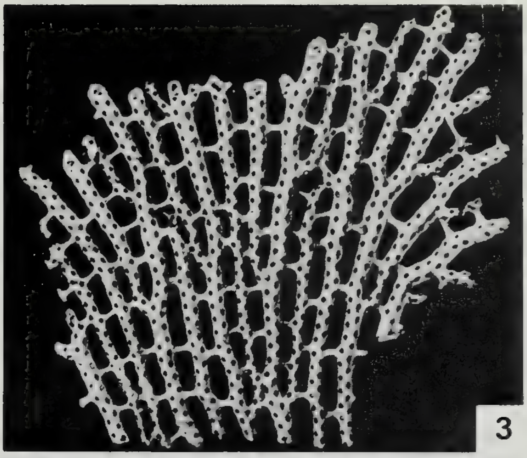
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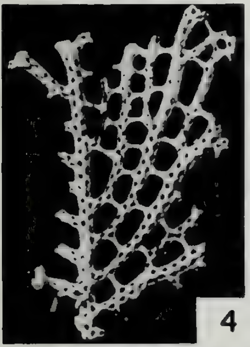
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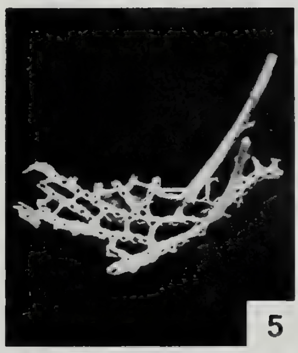
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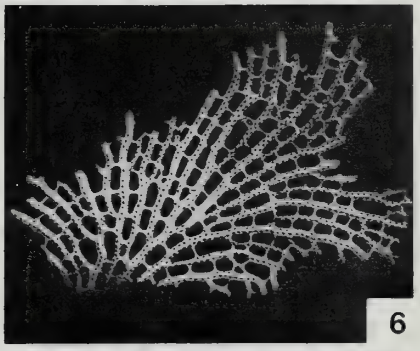
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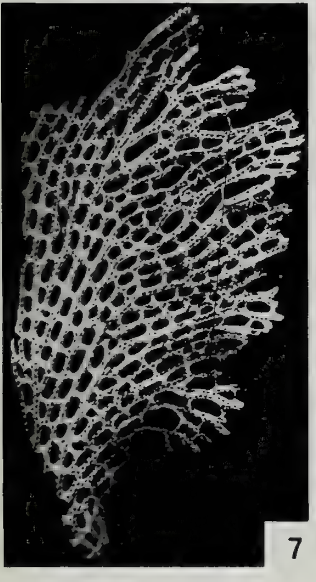
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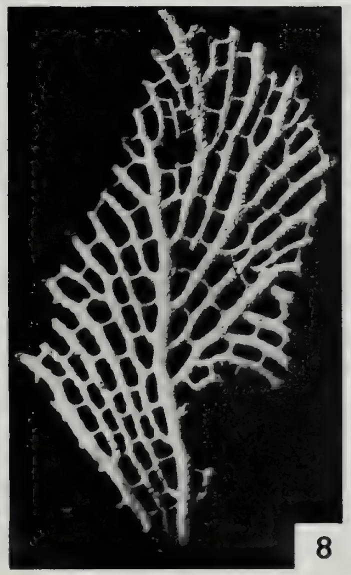
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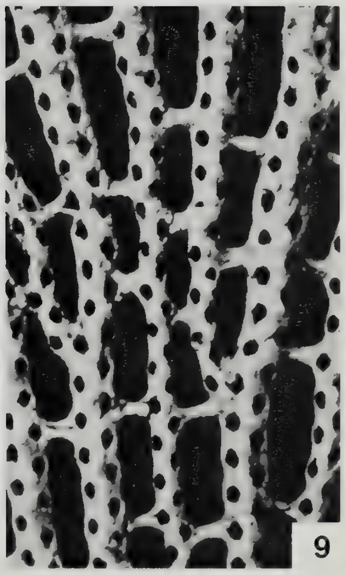
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PLATE 22

Hemitrypa hibernica M'Coy

FIG. 1. Proximal part of a colony attached to a *Rhombopora* fragment. Ends of supporting spines are visible. PD.4848. ×3·2.

FIG. 2. Reverse surface of zoarial fragment showing a secondarily thickened 'dissepimental arc'. PD.4849. ×3·5.

FIG. 3. Proximal part of a colony with enclosing superstructure and stout supporting spines. PD.4850. ×5·0.

FIG. 4. Obverse side with superstructure removed. PD.4851. ×5·0.

FIG. 5. Obverse with superstructure partly removed to show abnormal branching pattern, possibly a pathological condition. PD.4852. ×5·0.

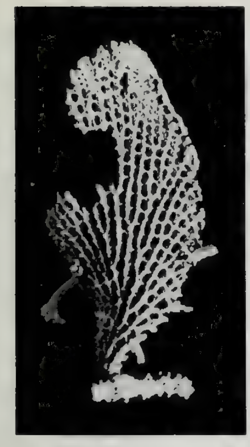
FIG. 6. Lateral view showing superstructure supported by carinal pillars. Underside of meshwork is encrusted by a *Fistulipora* colony. PD.4853. ×6·5.

FIG. 7. Reverse surface with distal parts of a long, branched supporting spine which reunites with the colonial meshwork. PD.4854. ×3·2.

FIG. 8. Obverse of a large fragment, with young *Fistulipora* colony encrusting the superstructure. PD.4855. ×3·0.

FIG. 9. Obverse of meshwork showing ovicellular concavities. PD.4856. ×4·4.

FIG. 10. Detail of obverse. PD.4857. ×18·0.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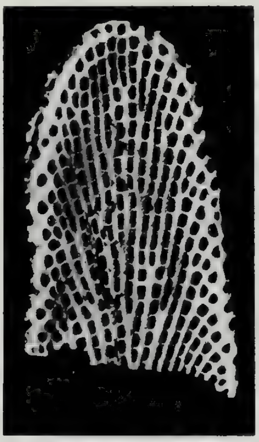
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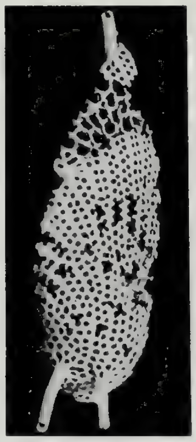
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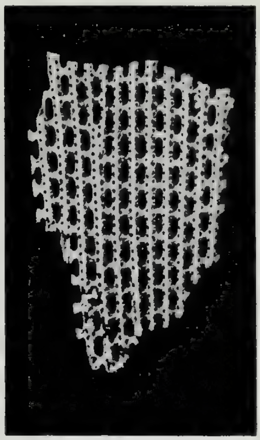
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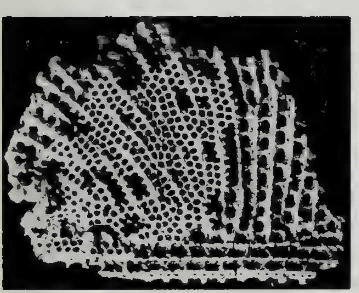
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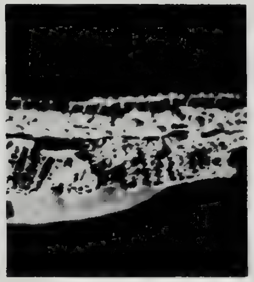
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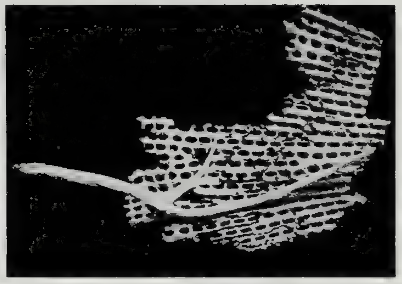
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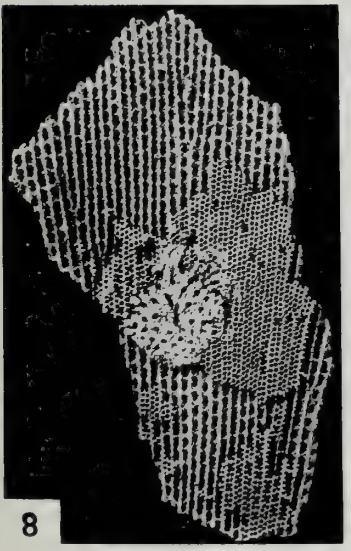
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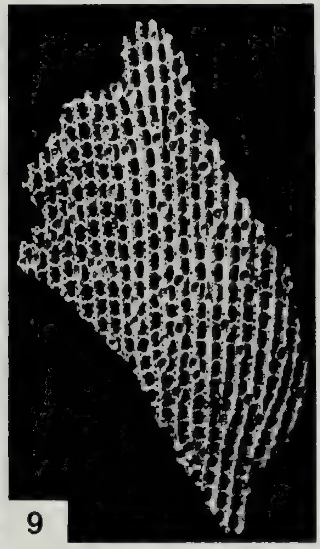
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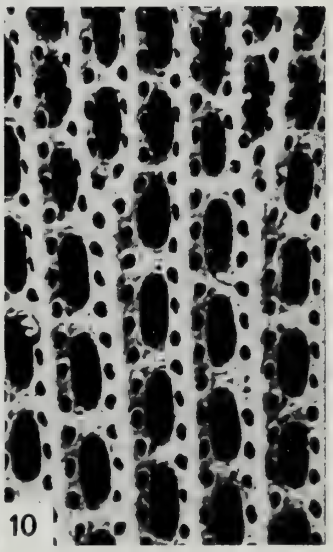
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PLATE 23

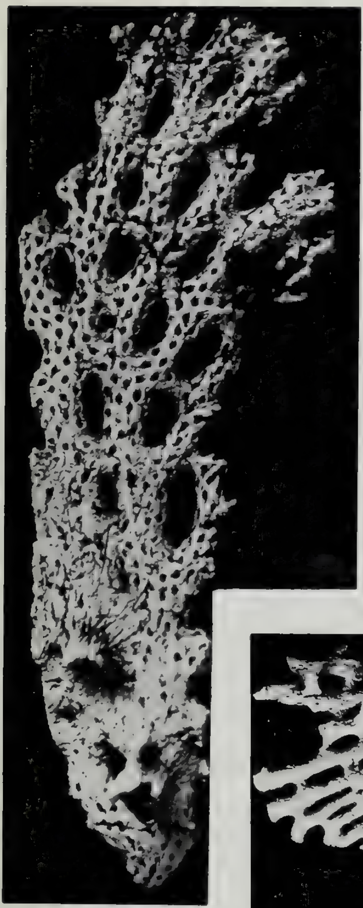
Polypora dendroides M'Coy

FIGS 1, 5. Obverse of zoarial fragments from the proximal parts of colonies. Thick secondary skeletal tissue is particularly evident at the bases of broken supporting spines, ×5·4; PD.4865, and PD.4866, ×2·6.

FIGS 3, 4. Reverse of meshwork. Fig. 4 shows the proximal parts of supporting spines. PD.4867, ×5·0; and PD.4868 ×2·6.

FIGS 2, 6. Obverse surfaces showing general characteristics of meshwork. PD.4867, ×5·0; and PD.4869, ×4·3.

FIG. 7. Detail of obverse side. PD.4867. ×13·0.



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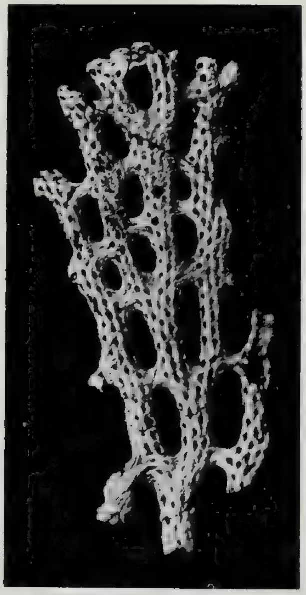

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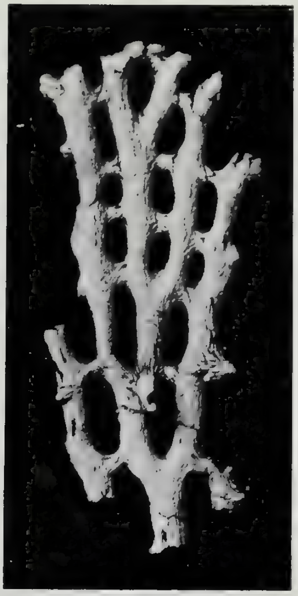

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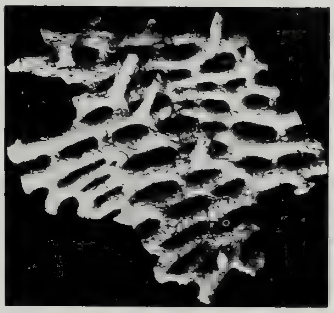

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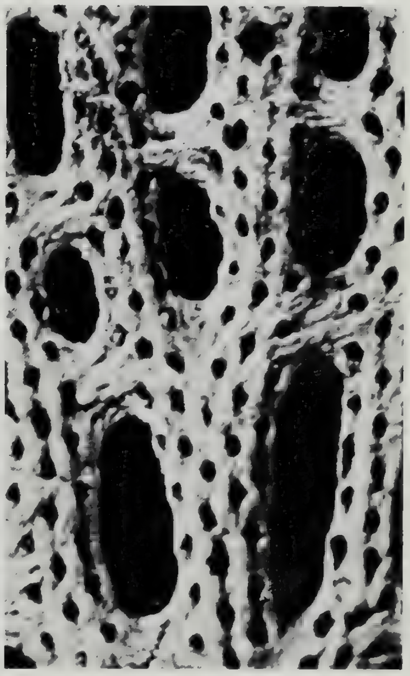

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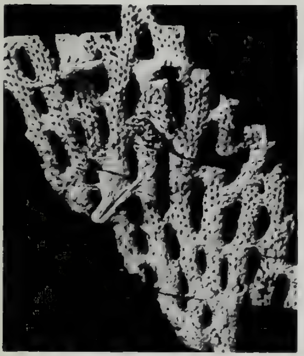

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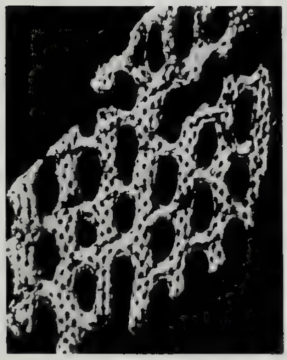

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PLATE 24

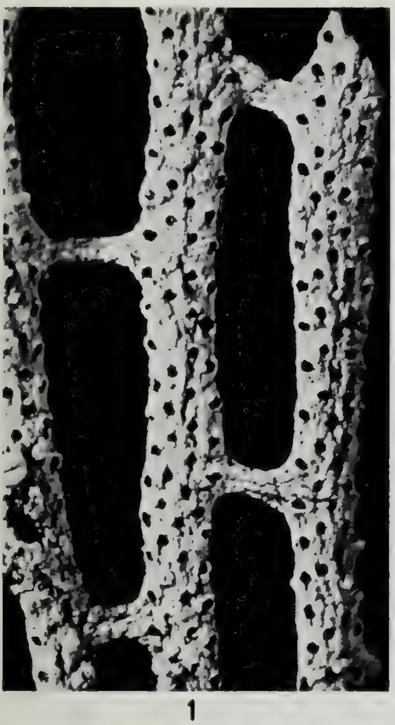
Polypora verrucosa M'Coy

FIG. 1. Detail of obverse. PD.4870. ×12·8.

FIGS 2, 3, 5, 7. Obverse of zoarial fragments showing general features of meshwork and branch surface. PD.4872, ×3·4; PD.4873, ×3·8; PD.4870, ×6·6; and PD.4874, ×6·2, respectively.

FIG. 4. Fragment from proximal part of a colony, showing prominent peristomes with terminal apertures, some of which are sealed by the thick secondary skeletal investment. PD.4871. ×6·6.

FIG. 6. Reverse side showing incipient beekitization resulting from the silicification of thick secondary skeletal accretions. PD.4877. ×6·0.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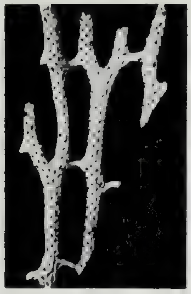
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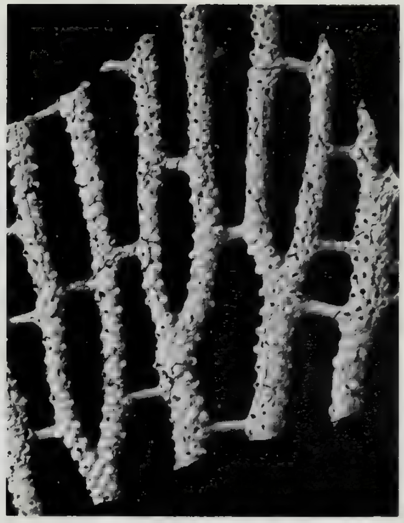
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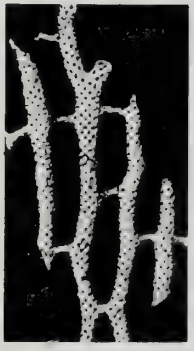
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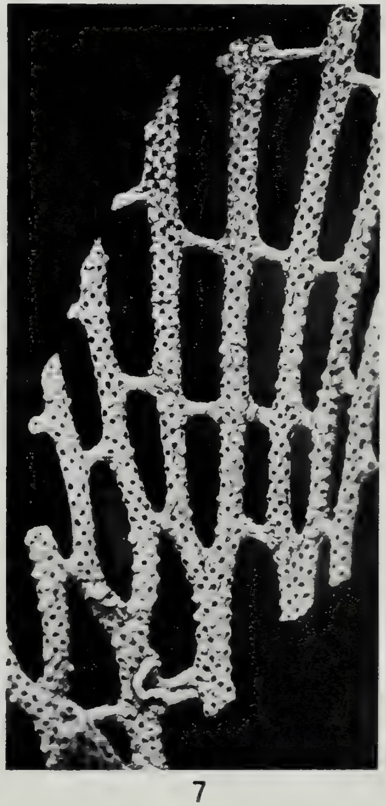
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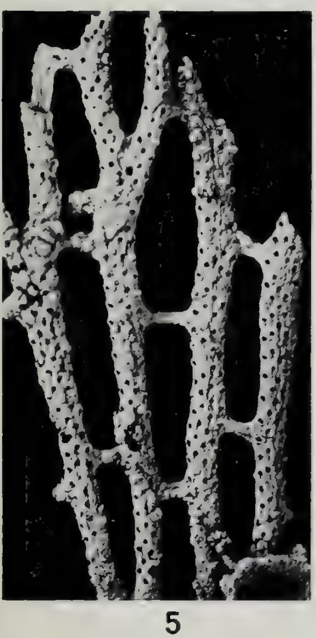
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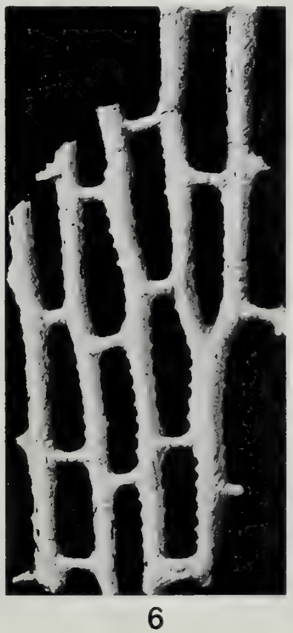
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PLATE 25

Ptylopora pluma M'Coy ***parva*** subsp. nov.

Fig. 1. Detail of obverse showing midrib and lateral branches. PD.4880 (paratype). ×18·6.

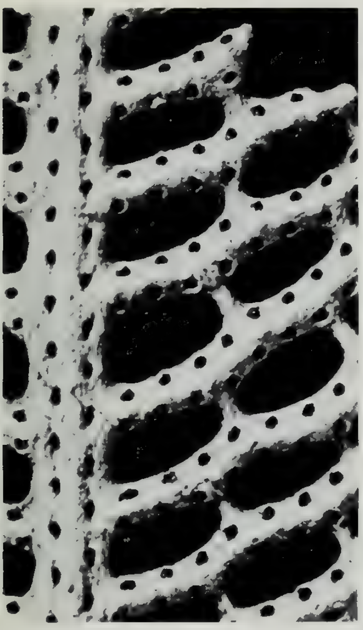
Fig. 2. Reverse surface with prominent 'striae'. PD.4880 (paratype). ×18·6.

Figs 3, 5, 8, 10. Obverse of zoarial fragments showing general meshwork characteristics. PD.4878, ×5·0; PD.4879, ×6·0; PD.4881 and PD.4882, ×4·1; ×4·1 (all are paratypes).

Fig. 4. Proximal part of a colony with thick outer secondary investment. The stalk-like holdfast has subsidiary attachment structures at its lower end. ×5·0.

Fig 6. Midrib of a colony with vestiges of secondary branches. PD.4883 (holotype). ×2·7.

Figs 7, 9. Reverse sides of zoarial fragments. Fig. 9 shows a short lateral spine developed from a branch end. PD.4884 and PD.4882 (paratype) respectively. Both ×4·1.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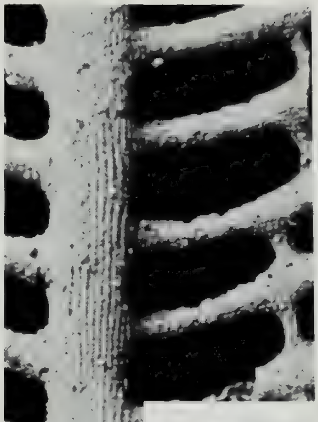
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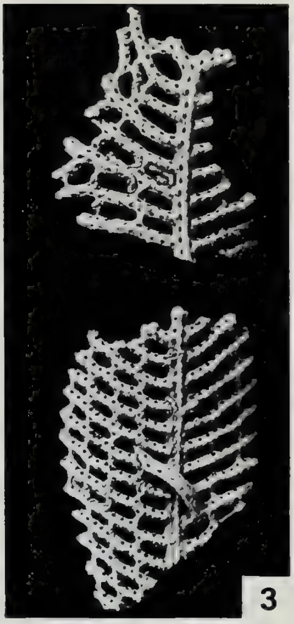
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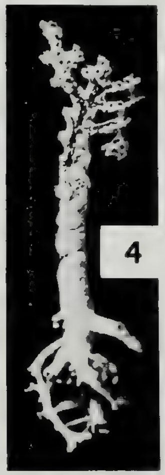
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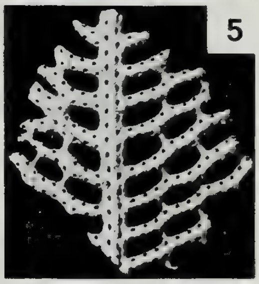
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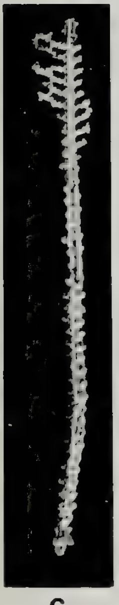
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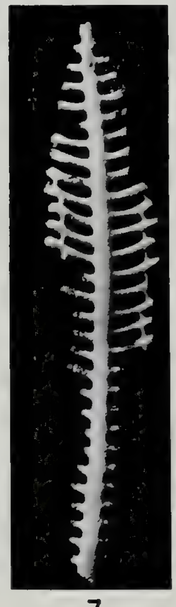
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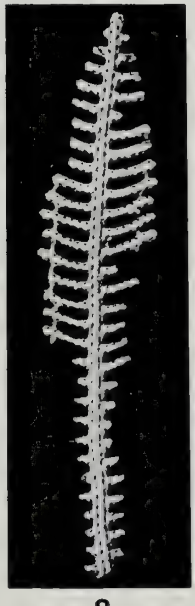
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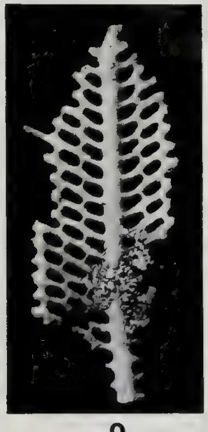
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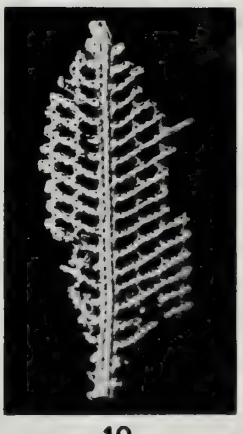
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PLATE 26

Septopora hibernica sp. nov.

FIGS 1, 7, 8. Obverse of zoarial fragments. In many places branch surfaces are obscured and zooecial apertures sealed by thick secondary skeletal deposits. PD.4885 (holotype), ×2·2; PD.4886 (paratype), ×6·1; and PD.4887 (paratype), ×3·6.

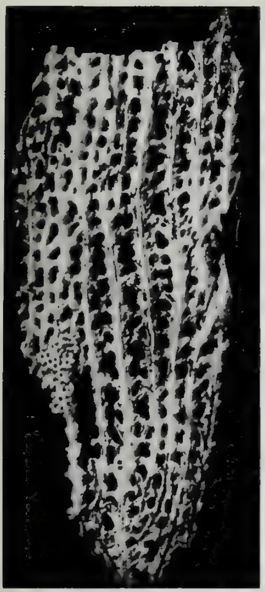
FIG. 2. Reverse surface of meshwork. The difference between primary and secondary branches is very marked. PD.4885 (holotype). ×2·2.

FIG. 3. Obverse with thick investment of secondary skeleton. The 'striae' traverse both branches and dissepiments when traced away from the bases of large spines. PD.4889 (paratype). ×4·5.

FIG. 4. Fragment with *Ptylopora*-like meshwork of midrib and lateral branches. PD.4888 (paratype). ×1·9.

FIG. 5. Zoarial fragments with irregular growth habit. PD.4890 (paratype) and PD.4891. ×4·5.

FIG. 6. Reverse surface showing thick deposits of secondary skeleton. PD.4889 (paratype). ×6·4.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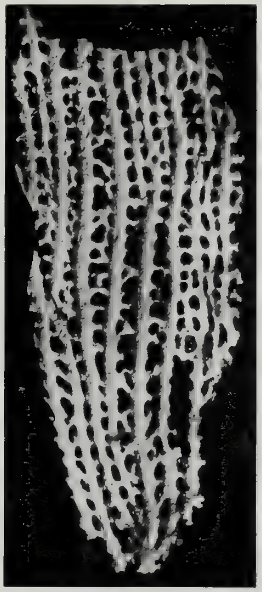
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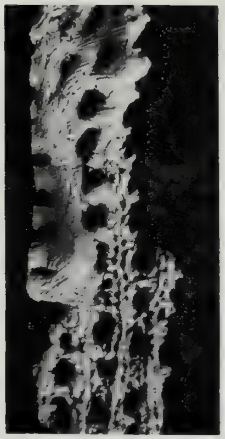
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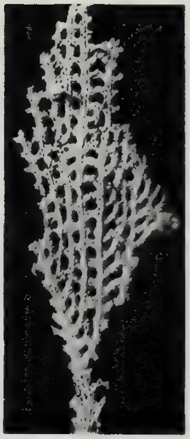
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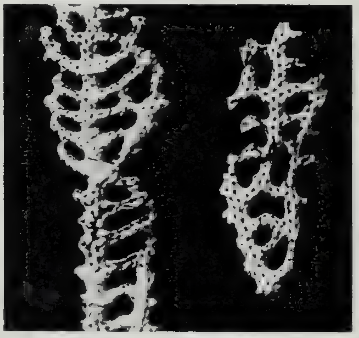
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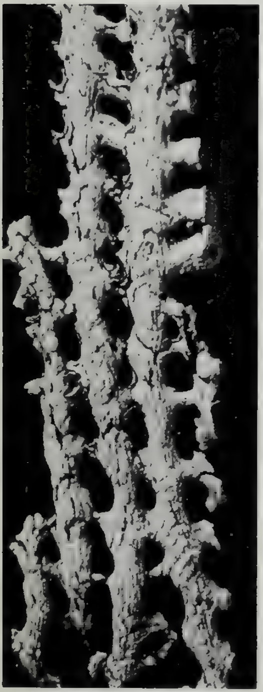
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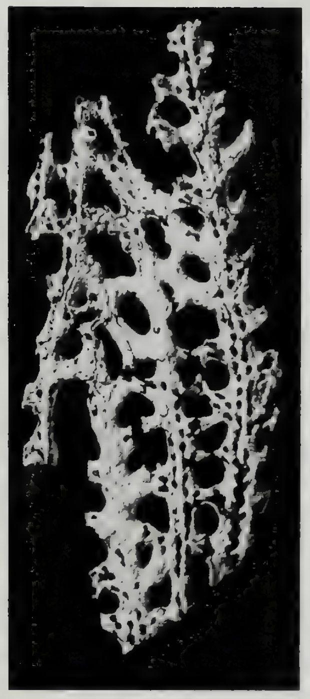
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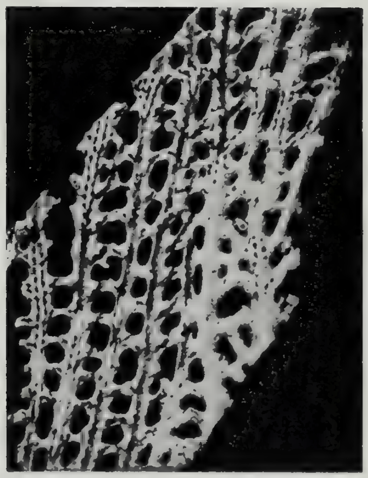
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2. El-Naggar, Z. R. Stratigraphy and Planktonic Foraminifera of the Upper Cretaceous—Lower Tertiary Succession in the Esna-Idfu Region, Nile Valley, Egypt, U.A.R. Pp. 291; 23 Plates; 18 Text-figures. 1966. £10.
3. Davey, R. J., Downie, C., Sargeant, W. A. S. & Williams, G. L. Studies on Mesozoic and Cainozoic Dinoflagellate Cysts. Pp. 248; 28 Plates; 64 Text-figures. 1966. £7.
3. Appendix. Davey, R. J., Downie, C., Sargeant, W. A. S. & Williams, G. L. Appendix to Studies on Mesozoic and Cainozoic Dinoflagellate Cysts. Pp. 24. 1969. 80p.
4. Elliott, G. F. Permian to Palaeocene Calcareous Algae (Dasycladaceae) of the Middle East. Pp. 111; 24 Plates; 17 Text-figures. 1968. £5.12½.
5. Rhodes, F. H. T., Austin, R. L. & Druce, E. C. British Avonian (Carboniferous) Conodont faunas, and their value in local and continental correlation. Pp. 315; 31 Plates; 92 Text-figures. 1969. £11.
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